

Taxonomy and Biology of *Megatrioza palmicola* Group (Homoptera: Psyllidae) in Hawaii^{1, 2}

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ABSTRACT

The generic status of *Megatrioza* Crawford is reviewed, and the importance of the immature stages in psyllid systematics, and in the systematics of Hawaiian *Megatrioza*, are discussed. *M. palmicola* Crawford is redescribed, based on adults of both sexes and immatures. Three new Hawaiian *Megatrioza* (*M. kauaiensis*, *M. molokaiensis* and *M. mauiensis*) are described, and keys to adults and nymphal stages of the Hawaiian species are provided. Biological data, including observations on courtship behavior, are also presented.

Generic Status of Megatrioza

There are about 32 described species of *Megatrioza* Crawford 1915, with the bulk of the species known from the eastern Palearctic, Indomalayan, Australian and Oceanian Realms. *Megatrioza* seems to be a polyphyletic taxon and the Hawaiian species treated in this study may not be properly placed in that genus. The generic status of *Megatrioza* has been surrounded by doubt, and, although a major taxonomic revision is needed, it is beyond the scope of this paper. However, a review of *Megatrioza* is provided.

Crawford (1915) proposed *Megatrioza* to accommodate a Philippine species, *M. armata* Crawford, and allied this genus to *Leuronota* Crawford 1914.

Based on the examination of 10 species of *Megatrioza* (which included undescribed species), Crawford (1918) determined the armed metatibiae and certain head and wing characteristics as significant in defining the genus. Although these species were known from the Malay Archipelago and Peninsula, the Philippines and Hawaii, he considered *Megatrioza* to be a Polynesian genus and speculated that many species remained to be discovered. He indicated that *Cerotriozia* Crawford 1918 with a new species, *C. bivittata* Crawford 1918 from Hawaii and 2 undescribed species from Borneo and Singapore, which he later described as *C. corniger* Crawford 1919 and *C. microceras* Crawford 1919, may be related to *Megatrioza*.

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Crawford (1919a) accounted for 12 species of *Megatrioza* with the known geographical range of the genus extending to Australia and Fiji, and speculated that more species would be discovered in tropical areas. Crawford noticed a tendency toward the reduction of the hindwings in *Megatrioza* and pointed out morphological similarities among *Megatrioza*, *Epitrioza* Kuwayama 1910, *Trioza* Foerster 1848, *Stenopsylla* Kuwayama 1910 and *Cerotrioza*. *Megatrioza* was distinguished from *Trioza* by differences in the metatibiae and he conjectured that *Trioza* was actively speciating in the North Temperate Zone, while most of the triozine species in the tropics and the South Temperate Zone were representative of the older genus *Megatrioza*. He considered *Epitrioza* to be a poorly defined genus because it possessed characteristics in common with *Trioza* and *Megatrioza*. The genera *Stenopsylla* and *Cerotrioza* both possessed armed metatibiae similar to *Megatrioza*, but *Cerotrioza* was believed to have sprung from *Megatrioza* and *Stenopsylla* was considered to resemble another genus, *Bactericera* Puton 1876. In the same paper, he referred a North American species, *Trioza diospyri* (Ashmead 1881), to the genus *Megatrioza* because of a resemblance to 2 Philippine species, *M. asiatica* Crawford 1915 and *M. magnicauda* Crawford 1919. Crawford (1920) transferred *C. corniger* and *C. microceras* to the genus *Leuronota* and described a new species, *Cerotrioza bridwelli*, from Hawaii.

Ferris (1926) synonymized *Megatrioza* with *Phylloplecta* Zacher 1913, because he found that *Psylla tripunctata* Fitch (=*T. tripunctata* (Fitch)), the type of the genus *Phylloplecta*, and *Megatrioza diospyri* (Ashmead) (=*Trioza diospyri* Ashmead) were congeneric because the major characteristics for *Megatrioza* was present in both species, but more strongly developed in *P. tripunctata*. Laing (1930) agreed with Ferris' decision and placed three representative species of *Megatrioza* in the genus *Phylloplecta*.

Tuthill (1943) disagreed with Ferris' (1926) observation that all of the generic characteristics of *Megatrioza* were strongly developed in *P. tripunctata* because of the weakly developed anterior and caudal metacoxal spines in that species. The large basal spur was also present in other genera and the presence of 2 inner apical spines were not considered to be significant generic characteristics. In addition, the basal spur on the metatibiae was absent in *M. diospyri*. Because *M. diospyri* and *P. tripunctata* appeared to be congeneric, Tuthill returned both species to *Trioza*, which contained other species with characteristics similar to *tripunctata*. Although Tuthill considered *Megatrioza* to be a natural group, based on the examination of a few specimens, he viewed it as being of subgeneric rank because most of the characteristics were variable, except for the number of apical spines, presence of basal spur on the metatibiae which varied in size, the presence of anteriorly directed metacoxal spurs and reduction of hindwings.

Zimmerman (1948) did not consider the well developed basal spur with a callused base on the base of the metatibiae in the Hawaiian *Megatrioza* as a significant generic characteristic because the calli in some Ha-

waiian species of psyllids were found to range from poorly to well developed, some with dentiform processes.

Concerning the separation of *Megatrioza* and *Phylloplecta* from *Trioza*, Mathur (1975) quoted L. R. Russell as having written, "I have examined about 25 species from different parts of the world and all specimens have metacoxal spurs though they are better developed in some species than others. They are present in *urticae*, the type species of *Trioza*, and in *tripunctata*, the type of *Phylloplecta*. Therefore this character cannot be used to separate the two and I do not know of other characters that can be used for this purpose." Mathur, out of convenience, divided the genus *Trioza* into 2 subgroups, with *Phylloplecta* and *Megatrioza* combined in the *Phylloplecta* subgroup, and *Trioza* (sensu stricto) in the *Trioza* subgroup.

In Hollis' (1984) treatment of Afrotropical psyllids, he reviews the distribution of the genera of *Triozidae* and includes *Megatrioza* in the genus *Trioza*.

Megatrioza Endemic to the Hawaiian Islands

Crawford (1918) described *M. palmicola* from specimens which had been collected on a fan-palm, *Pritchardia* sp. (Palmae), from Punaluu in the Koolau Mountains on Oahu island. He conjectured that *M. palmicola* was endemic to Hawaii because of its presence on native species of *Pritchardia* and its absence on cultivated palms at lower elevations. He speculated that an immigrant ancestor gave rise to *M. palmicola* independently of other native psyllids because its ancestral species arrived in Hawaii at a later time and became adapted to a free-living habit on the folds of the younger leaves of *Pritchardia*.

Swezey (1919) observed that the psyllid nymphs of *Megatrioza* collected from Glenwood on Hawaii island were free-living on *Pritchardia* leaves and produced wooly wax. Crawford (1919b) examined specimens of nymphs and adults of *Megatrioza* collected by Swezey and determined these specimens to be the same or a variation of *palmicola*. The immatures were characterized as having enlarged marginal hairs or projections. Crawford (1928) described *Megatrioza mallotica* from Sumatra and noticed similarities with *M. palmicola*, but considered it different.

Zimmerman (1948) examined determined specimens of *M. palmicola* collected from Kauai and Hawaii islands and considered these to be undescribed forms. He speculated that the Hawaiian species of *Megatrioza* were derived from the Hawaiian *Trioza* or of another origin, but conceded that other species of *Megatrioza* were known from the South Pacific Islands of Samoa and Fiji. Furthermore, L. M. Nakahara (pers. comm.) found that the immature stages of Hawaiian species of *Trioza* and *Megatrioza* have distinct differences in the shape and number of setasetae which may be of specific significance, regardless of morphological similarities of the adults.

Taxonomic Importance of Immature Stages

During 1862-1888, Loew used illustrations and biological studies on the immature stages of psyllids to differentiate between morphologically similar species which, in some cases, were considered as varieties by other workers (Klimaszewski 1964).

Sulc, during the early 1900's, made morphological species descriptions and included illustrations of adult characters which had diagnostic value. These characters became widely accepted so that studies on the biology of psyllids and immature development were no longer considered as necessary by other workers in making taxonomic decisions (Klimaszewski 1964).

Crawford (1914) recognized the importance of collecting adults as well as nymphs of psyllids, but a classification based on the immatures was impossible at that time because of the limited amount of information that existed on the known species of psyllids.

During the 1920's, Ferris (Ferris 1923, 1924, 1925, 1926, 1928a, 1928b; Ferris & Hyatt 1923) produced a series of works in which he established a suitable format for the descriptions of immature psyllids and included illustrations to aid in the identification of species when the adult stage was unavailable. Ferris (1925) recognized two general immature forms, the triozine and psyllinae forms, which were characteristic of the subfamilies Triozinae and Psyllinae respectively.

Klyver (1930, 1931) continued Ferris' trend, but with the intention of describing the nymphs of different generic and subfamily types so that a general classification could be attained by combining the classification of psyllids, which was based solely on the adult stages, with the information gathered on the immature stages. Unfortunately his work was curtailed abruptly.

Rahman (1932) not only recognized the importance of studying the immature stages from the standpoint of taxonomy, but also from that of control because at that time it was difficult to identify the immatures of some common pest species. He recognized a third immature form, the pauropsyllinae type, which was characteristic of the subfamily Pauropsyllinae.

Klimaszewski (1964) emphasized the importance of relating immature morphology with that of the adults in solving the current problems on the evolutionary relationships of psyllids. The number of free sclerites, wingpad shape and antennal structures were considered as important for this purpose. At the species level, the number and distribution of marginal spines, structure of the circumanal pore ring, and microstructure and form of the spiracles were found to be useful taxonomic characteristics because they undergo adaptive changes at a much slower rate than other morphological characters.

White and Hodkinson (1985) stressed the importance of utilizing data on nymph and adult characteristics for producing a classification which can accommodate still unknown tropical and temperate psyllids.

MATERIALS AND METHODS

Eggs, nymphs and adults of *Megatrioza* were collected in the field from April 1979 to November 1981 on the islands of Kauai, Oahu, Molokai and Maui.

Specimens collected on islands other than Oahu were difficult to keep alive when removed from their host plant for more than two days. Specimens collected in the field were thus kept in capture vials and, upon return from the field, were stored at 16.7 to 22.2°C in a foam cooler which contained "Blue Ice" wrapped in several layers of newspaper. In this way, most of the adults and immatures could be kept alive for at least 3 days.

Seeds of *Pritchardia* sp. were collected from the yards of the Cockett's and Desha's from Lanai City on Lanai island, and seeds of *Pritchardia affinis* Beccari were collected at Keauhou Harbor on Hawaii island. Seedlings grown to a height of about 0.3 m were used to rear *Megatrioza*.

Specimens of *Megatrioza* were introduced onto the leaf of the palm seedlings and either the entire seedling or a leaf was enclosed within a plastic bag with organdy sewn to the closed end to prevent moisture condensation. Cotton was wrapped around the petiole of each leaf or around the base of the palm seedlings. The open end of the plastic bag was taped tightly around the cotton, which served as a barrier to prevent the escape of the psyllids and exclude other insects. Each seedling was placed in a 10 gallon aquarium covered with a single sheet of organdy and maintained at 80% relative humidity at 24.9°C. Attempts to rear adults in wooden screen cages under laboratory conditions of 69% relative humidity and 23.5°C were unsuccessful.

Mating behavior was observed under a dissecting microscope by allowing a field collected male and female to move into a 7 × 34 mm plastic vial cap taped to the inside of a petri dish cover. Because mating usually took place under low intensity light, most of the lights in the laboratory were turned off during observation. Once the mating commenced, the microscope illuminator was used at low light intensity to improve visibility. Observations of egg laying were made through the plastic bag which enclosed the entire seedling.

Hatching, feeding and molting of nymphs were observed on the palm seedling using a dissecting microscope. The behavior of the nymphs was difficult to observe because they are negatively phototropic and feed in the folds or deep in the axils of the leaves.

TAXONOMY Species Groups of Hawaiian *Megatrioza*

The 4 species of *Megatrioza* (*M. palmicola* Crawford, *M. kauaiensis* n. sp., *M. molokaiensis* n. sp. and *M. mauiensis* n. sp.) treated in this paper form a natural group of species which is here referred to as the *Megatrioza palmicola* group. Collections of the *M. palmicola* group were made from the Northwestern Hawaiian island of Nihoa and the major islands of Lanai

and Hawaii. Another group of 3 other species which appears related to the *M. palmicola* group was collected on *Pritchardia* spp. from the islands of Molokai, Maui, Lanai and Hawaii. However, a complete collection of all stages is needed before these species can be properly characterized and described.

All measurements are given in millimeters. Holotypes of the new species are in the Bishop Museum, Honolulu, Hawaii and the paratypes in the collection of the senior author.

Generic Placement of *Megatrioza palmicola*

Examination of 3 specimens including 2 cotypes, of *Megatrioza armata* (Fig. 1, A), indicated that *M. palmicola* (Fig. 1, B) may not be properly placed in the genus *Megatrioza*. Although *M. palmicola* possessed the characteristics of *Megatrioza* as given in Crawford's (1918) type description, the structure of the head and forewings are so different as to preclude its placement in *Megatrioza*. The head of *M. armata* (Fig. 1, C) is declivous, the genal cones are long, divergent, subporrect and thickest in the middle and the anterior ocellus is visible from above. The forewings are acute at the apex. By contrast, the head of *M. palmicola* (Fig. 1, D) is deflexed with short, divergent and subacute genal cones which project ventrally, and the anterior ocellus is visible from the front. The forewings are obtuse at the apex, resembling the forewings of the Hawaiian *Trioziinae*. *M. palmicola* appears to represent another genus, but no attempt to establish a new genus or remove it from *Megatrioza* will be made until a generic revision can be undertaken.

Crawford (1915), based his original description of *M. armata* on a single male and a single female specimen. However, 1 male and 2 female specimens are present in the USNM. Because the cotypes were not properly labeled, the female: Butuan, Mindanao Baker; 3238; 1943 Colln. D. L. Crawford; is designated as lectotype. One forewing, which was missing, was probably used by Crawford (1915, Pl. 1, Fig. d) for his drawing.

The male specimen: Butuan, Mindanao Baker; 1943, Colln. D. L. Crawford; is designated paralectotype. This specimen is badly damaged. The flagella of both antennae are missing, the thorax is broken in half between coxae II and III, the left mesoleg, distal segment of left metatarsi and right hindwing are missing.

The other female specimen is labeled: Butuan, Mindanao Baker; 3238; C. F. Baker Coll. 1927; *Megatrioza armata* Crawf. Although this specimen bears a red determination label, it seems likely that it was held in Baker's collection, rather than being one of the type specimens held by Crawford. The broken tip of the left forewing is retained with the specimen.

KEY TO ADULTS OF MEGATRIOZA PALMICOLA GROUP

1. Markings on head and thorax (Fig. 11, B); aedeagus spoon-shaped (Fig. 5, B) (Kauai island) *M. kauaiensis* n. sp.
- Markings on head and thorax (Figs. 11, A, C, D); aedeagus capitate (Fig. 5, A) 2
2. Wings translucent, with whitish cast; markings on head and thorax (Fig. 11, A) (Oahu island) *M. palmicola* Crawford
- Wings transparent, without whitish cast 3
3. Markings on head and thorax (Fig. 11, C) (Molokai island)
- *M. molokaiensis* n. sp.
- Markings on head and thorax (Fig. 11, D) (Maui island)
- *M. mauiensis* n. sp.

KEY TO NYMPHAL STAGES AND SPECIES OF MEGATRIOZA PALMICOLA GROUP

FIRST INSTAR. Length 0.51-0.59; width 0.29-0.34; margin of meso-, metathorax (Figs. 12, A-D) with flattened spine-like projections; antennae (Figs. 3, A, F) one segmented, with 3 setae (including specialized seta), 2 sensoria.

KEY TO FIRST INSTAR

1. Sectasetae (Figs. 6, B, C, D; 12, A, E, I, M) stout, apices emarginate; circumanal pore ring (Figs. 6, E, F; 12, M) *M. palmicola* Crawford
- Sectasetae lanceolate, apices acute, apical section of sectasetae may be nearly linear 2
2. Flattened spine-like projections (Fig. 12, D) on margin of meso-, metathorax, length about as long as basal width; circumanal pore ring (Fig. 12, P) *M. mauiensis* n. sp.
- Flattened spine-like projections on margin of meso-, metathorax, length about 2 to 3 times as long as basal width 3
3. Flattened spine-like projection (Fig. 12, B) length about 3 times as long as basal width; circumanal pore ring (Fig. 12, N) *M. kauaiensis* n. sp.
- Flattened spine-like projection (Fig. 12, C) length about 2 times as long as basal width; admarginal sectasetae on cephaloprothorax (Fig. 12, G) narrowly lanceolate, with distal section nearly linear, unlike rest of admarginal sectasetae (Figs. 12, C, K, O); circumanal pore ring (Fig. 12, O) *M. molokaiensis* n. sp.

SECOND INSTAR. Length 0.86-0.98; width 0.60-0.71; antennae (Figs. 3, B, G) two segmented, with 3 setae (including specialized seta), 3 sensoria; abdomen (Fig. 7, A) with longitudinal row of ventral setae submedially on each side.

KEY TO SECOND INSTAR

1. Body (Figs. 7, B, C, D; 13, A, E, I, M, Q) with admarginal row of stout sectasetae, apices emarginate; circumanal pore rings (Figs. 7, E; 13, Q) *M. palmicola* Crawford
Body with admarginal row of lanceolate sectasetae or simple setae 2
2. Wingpads (Fig. 13, B) with admarginal row of setae; circumanal pore rings (Fig. 13, R) *M. kauaiensis* n. sp.
Wingpads (Figs. 13, C, D) with admarginal row of lanceolate sectasetae 3
3. Sectasetae on cephaloprothorax (Fig. 13, G) admarginal, narrowly lanceolate, with distal section nearly linear, unlike rest of admarginal sectasetae (Figs. 13, C, K, O, S); circumanal pore rings (Fig. 13, S) *M. molokaiensis* n. sp.
Sectasetae on margin of cephaloprothorax (Fig. 13, H), wingpads (Fig. 13, D), abdomen (Figs. 13, L, P, T) admarginal, lanceolate, with distal section angular; circumanal pore rings (Fig. 13, T) *M. mauiensis* n. sp.

THIRD INSTAR. Length 1.28-1.62; width 0.97-1.22; antennae (Figs. 3, C, H) two segmented with 4 setae (including specialized seta), 4 sensoria; abdomen (Fig. 8, A) with transverse row of ventral setae across each segment.

KEY TO THIRD INSTAR

1. Cephaloprothorax (Figs. 8, B; 14, E), wingpads (Figs. 8, C; 14, A) with admarginal row of spatulate setae; circumanal pore rings (Figs. 8, E; 15, A) *M. palmicola* Crawford
Cephaloprothorax (Figs. 14, F-H), wingpads (Figs. 14, B-D) with admarginal row of simple setae which may be mixed with lanceolate sectasetae 2
2. Posterior wingpads (Fig. 14, B) with admarginal row of setae; circumanal pore rings (Fig. 15, B) *M. kauaiensis* n. sp.
Posterior wingpads (Figs. 14, C, D) with admarginal row of setae mixed with sectasetae 3
3. Cephaloprothorax (Fig. 14, H) with reduced dorsal setae, with small dorsal seta with enlarged base on each side; circumanal pore rings (Fig. 15, D) *M. mauiensis* n. sp.

- Cephaloprothorax (Fig. 14, G) with longer dorsal setae, with greatly enlarged dorsal seta on each side (trichome not illustrated); circumanal pore rings (Fig. 15, C)
..... *M. molokaiensis* n. sp.
- FOURTH INSTAR.** Length 2.07-2.67; width 1.53-1.90; antennae (Figs. 3, D, I) three segmented with 7 setae (including specialized seta), 5 sensoria.

KEY TO FOURTH INSTAR

1. Cephaloprothorax (Figs. 9, B; 16, E), wingpads (Figs. 9, C; 16, A), sides of abdomen (Figs. 9, D; 16, M) with admarginal row of spathulate setae, posterior margin of abdomen (Figs. 9, E; 16, I) with admarginal row of sectasetae; circumanal pore rings (Figs. 9, F; 17, A)
..... *M. palmicola* Crawford
- Cephaloprothorax (Figs. 16, F-H), wingpads (Figs. 16, B-D) with admarginal row of simple setae; abdomen (Figs. 16, J-L, N-P) with 2 submarginal rows of sectasetae 2
2. Cephaloprothorax (Figs. 16, F, G) with enlarged dorsal seta on each side 3
- Cephaloprothorax (Fig. 16, H) with reduced dorsal setae, relatively enlarged seta with enlarged base on each side; circumanal pore rings (Fig. 17, D) *M. mauensis* n. sp.
3. Wingpads (Fig. 16, B) with longitudinal row of dorsal setae near margin, length about as long as admarginal setae; circumanal pore rings (Fig. 17, B) *M. kauaiensis* n. sp.
- Wingpads (Fig. 16, C) with longitudinal row of dorsal setae near margin, length about 1/3 as long as admarginal setae; circumanal pore rings (Fig. 17, C) ... *M. molokaiensis* n. sp.

FIFTH INSTAR. Length 3.40-4.50; width 2.45-3.35; antennae (Figs. 3, E, J) six segmented with 10 setae (including specialized seta), 5 sensoria.

KEY TO FIFTH INSTAR

1. Margin of cephaloprothorax (Figs. 10, B; 18, E), wingpads (Figs. 10, C; 18, A), sides of abdomen (Figs. 10, D; 18, M) with admarginal row of spathulate setae; circumanal pore rings (Figs. 10, F; 19, A) *M. palmicola* Crawford
- Margin of cephaloprothorax (Figs. 18, F-H), wingpads (Figs. 18, B-D), sides of abdomen (Figs. 18, N-P) with admarginal row of lanceolate sectasetae or simple setae 2

2. Cephaloprothorax (Fig. 18, H) with enlarged dorsal seta wanting on each side; circumanal pore rings (Fig. 19, D) *M. mauiensis* n. sp.
- Cephaloprothorax (Figs. 18, F, G) with greatly enlarged dorsal seta on each side..... 3
3. Wingpads (Fig. 18, B) with longitudinal row of dorsal setae near margin, length about as long as or longer than admarginal setae; circumanal pore rings (Fig. 19, B) *M. kauaiensis* n. sp.
- Wingpads (Fig. 18, C) with longitudinal row of dorsal setae near margin, length less than 1/2 as long as admarginal setae; circumanal pore rings (Fig. 19, C) .. *M. molokaiensis* n. sp.

Species Descriptions

Terms and description style follows Ferris (1924), Miyatake (1964), Mathur (1975), Hodkinson & White (1979) and White and Hodkinson (1982).

Adult morphology of most of the species of the *M. palmicola* group are similar and can only be separated by differences in markings. Therefore a complete description of color of the adults are given. For a description of the morphology of adults, refer to Crawford 1918.

A complete description of nymphal morphology of the *M. palmicola* group is given in the redescription of *M. palmicola*. Diagnostic characteristics of the nymphs of *M. palmicola* are enclosed in brackets []. Descriptions of 3 new species include only the most important characteristics that are not in common with *M. palmicola*. Characteristics of first instar nymph which are common to later instars of the same species, are not repeated; thus only different characteristics are given.

Megatrioza palmicola Crawford

(Figs. 2, A-C; 3, A-J; 4, A-E; 5, A-B; 6, A-F; 7, A-D, E; 8, A, E; 9, A, F; 10, A, F; 11, A; 12, A-D; i3, A-D, E-H, I, M, Q-T; 14, A, E; 15, A-D; 16, I, M; 17, A-D; 19, A; 20, A).

Megatrioza palmicola Crawford, 1918. Proc. Hawaii. Entomol. Soc. 3:452.

ADULT STAGE

Diagnosis. *M. palmicola* (Fig. 11, A) with three longitudinal streaks on thorax. Capitate aedeagus (Fig. 5, A) differs from spoon-shaped aedeagus (Fig. 5, B) of *M. kauaiensis*.

Male. Color. General color light brown with brown markings. *Head* (Fig. 11, A). Vertex brown along posterior margin, not extending laterally beyond foveal depressions; foveal depressions pale orange; dorsal ocelli red, anterior ocellus light brown (probably due to loss of color); genal cones brown; clypeus brown; eyes mottled black with light brown (mottling probably due to discoloration); antennal segments IV-X brown.

Thorax (Fig. 11, A). Pronotum brown with darker brown band along anterior margin, darker brown longitudinal submedial streak on each side; mesothoracic prescutum, scutum brown with 3 poorly defined darker brown longitudinal streaks; mesothoracic scutellum brown with dark brown W-shaped mark; mesothoracic pleura, sternum brown. **Wings.** Translucent with whitish cast, basal 1/2 smoky brown, radular spinules brown; veins brown proximally, becoming light brown distally along basal 1/2 of wing R+M+Cu, R, Cu₁, Cu₂, bases of M, Cu₁, hind margin adjacent radular spinules brown. **Legs.** Light brown; pro-, mesotibiae brown apically; pro-, mesotarsal segments brown; metatibiae with brown lateral streaks on each side, genual spine of metatibiae light brown, outer subapical, inner apical saltatorial spines of metatibiae black apically. **Abdomen.** Brown, proctiger brown anteriorly; parameres brown apically.

Female apparently teneral, fitting description of male except for following: **Head.** Vertex light brown along posterior margin; eyes black. **Thorax.** Light brown dorsally. **Wings.** Faint smoky brown spots anteriorly along R+M+C near junction, along hind margin at distal end of A, adjacent radular spinules. **Legs.** Pro-, mesotibiae light brown; metatibiae with brown genual spur. **Abdomen.** Light brown; most abdominal segments brown anteriorly; proctiger with brown band basally, subgenital plate brown apically.

IMMATURE STAGES

EGG (Fig. 20, A).

Dimensions. Length 0.48; width 0.14.

FIRST INSTAR.

Dimensions. Length 0.51-0.59, [0.53-0.59]; width 0.29-0.34, [0.30-0.34].

Shape (Fig. 6, A). Elliptical; head fused with prothorax; meso-, metathorax weakly defined, laterally produced, wingpads undefined; abdomen well defined.

Margin (Fig. 6, A). Flattened spine-like projections present, one on each side of cephaloprothorax (Fig. 6, A) anterior to posterior most admarginal setaseta, in row on meso-, metathorax (Figs. 12, A-D), [length (Figs. 6, A, C; 12, A) about 2 times as long as basal width].

Dorsum (Fig. 6, A). **Sclerotization.** Weakly sclerotized; cephaloprothorax with unsclerotized irregular shaped area, rectangular shaped area near lateral margin of meso-, metathorax (not illustrated) on each side; sclerites of head fused with thorax on each side, lateral halves separated medially by narrow membranous region; metathoracic sclerites separated from abdominal sclerites by narrow transverse intersegmental membrane; abdomen with 7 segmented caudal plate, segmentation weakly defined, lateral halves separated medially by narrow membranous region except for medially fused posterior segment. **Indumentum** (Fig. 6, A). Body (Figs. 12, [A]-D, [E]-H, [I]-L, [M]-P) with admarginal row of [relatively stout, emarginate, dorsoventrally compressed] setasetae, borne on

strongly developed protuberances; abdomen with 26 setasetae. Setae simple, sparse, mostly small; [cephaloprothorax (Fig. 12, E) with greatly enlarged submarginal seta on each side]; cephaloprothorax, thorax with several dorsal setae forming 2 longitudinal rows on each side; abdomen with 1 submedial seta on basal segment on each side, 1 medial seta on terminal segment (not illustrated), submarginal row (Figs. 12, I-L) of 5 dorsal setae on each side with 1 or 2 posterior setae enlarged. *Cuticular structures.* Small, convex, blister-like protuberances (Fig. 2, B) may be present on dorsum. Spinules (Fig. 2, A) arranged in short submedian transverse band on each side of meso-, metathoracic segments, in narrow band extending almost completely across each abdominal segment. Subelliptical structures (Fig. 2, B) submedial on each side of meso-, metathorax, between each abdominal segment, each containing dot-like structures. Minute points (Fig. 2, C) sparse near apex of abdomen.

Venter (Fig. 6, A). *Sclerotization.* Unsclerotized except for cuticular structures, circumanal pore ring plate (not illustrated). Cephaloprothoracic, thoracic, abdominal sclerites completely fused, segments poorly defined. *Indumentum.* Setae simple, sparse, mostly small; cephaloprothorax with 2 setae on each side, subequal in length; clypeus with 1 basal setae on each side; abdomen with 1 submedial seta on basal segment on each side, circumanal pore ring (Figs. 12, M-P) surrounded by 3 setae on each side, 1 anterior, 2 posterior. *Cuticular structures.* Minute points numerous, densely distributed on venter. Spinules arranged in irregular transverse band extending across medial region of each abdominal segment, surrounded by minute points. *Antennae* (Figs. 3, A, F). Relatively short, ventral, one segmented; 3 setae, 1 blunt apical seta, 1 long subapical seta, 1 specialized medial seta borne on ridge that spirals on inside of cup-shaped sensorium-like receptacle; 2 sensoria, 2 subapical with 1 dorsal, 1 ventral. *Clypeus.* Pair of small basal setae. *Labium.* Two pairs minute setae on basal segment. *Legs.* Relatively short; trochanter undefined; femora not reaching margin of body; tibiotarsal articulations absent (Fig. 4, A); claws present (not illustrated); pulvilli subelliptical; armed with setae, subequal in size, sparse, 1 long capitate seta with bent apex at distal end of each tibiotarsus; spinules sparse; pair of sensoria at base of each femora, 1 sensorium near anterior margin of each tibiotarsus. *Circumanal pore ring* (Figs. 12, [M]-P). Ventral. [Configuration of pores variable (Fig. 6, E-F)].

SECOND INSTAR.

Dimensions. Length 0.86-0.95, [0.86-0.98]; width 0.60-0.71, [0.60-0.68].

Shape (Fig. 7, A). Obovate; cephaloprothorax produced anteriorly; cephaloprothorax, anterior, posterior wingpads differentiated by weakly incised margin.

Margin (Fig. 7, A). Serrate. Flattened spine-like projections absent.

Dorsum (Fig. 7, A). *Sclerotization.* Entirely sclerotized, cephaloprothorax well defined by U-shaped suture (not illustrated). *Indumentum.* Body (Figs. [7, A-D]; 13, [A]-D, [E]-H, [I]-L, [M]-P, [Q]-T) with

[relatively stout] sectasetae borne on weakly developed protuberances in admarginal row, setae may be present. Cephaloprothorax, thorax with few small setae scattered among smaller setae; abdomen with few setae; [dorsal setae reduced in size, cephaloprothorax (Fig. 13, E) with relatively large seta with enlarged base on each side]; anterior, posterior wingpads (Figs. 13, A-D) with longitudinal row of dorsal setae near margin on each side. *Cuticular structures.* Spinules sparse, forming comb-like structures arranged in interrupted transverse band on each abdominal segment, clustered near apex.

Venter (Fig. 7, A). *Sclerotization.* Abdominal segments each with narrow sclerotized regions (not illustrated) extending transversely across medial area of abdomen along posterior margin of each segment, posterior to band of spinules; spiracular, circumanal pore ring plates sclerotized. *Indumentum.* Setae subequal in length; cephaloprothorax with 4 ventral setae on each side; abdomen with 6 submedial setae in longitudinal row, 4 setae in submarginal row on each side, circumanal pore ring surrounded by 5 setae on each side (Figs. 13, Q-T), 2 anterior, 1 lateral, 2 posterior. *Antennae* (Figs. 3, B, G). Two segmented; basal segment with dorsal sensorium, apical segment resembling antennae of first instar. *Legs* (Fig. 4, B). *Circumanal pore rings* (Figs. [7, E]; 13, [Q]-T).

THIRD INSTAR.

Dimensions. Length 1.28-1.62, [1.28-1.62]; width 0.97-1.22, [0.97-1.17].

Dorsum (Fig. 8, A). *Indumentum.* [Cephaloprothorax (Fig. 14, E), wingpads (Fig. 14, A) with spathulate setae in admarginal row]. Setae numerous; smaller setae more abundant on cephaloprothorax, wingpads, abdomen; larger setae less numerous, more abundant on thorax; abdomen with more than 5 setae in row near margin.

Venter (Fig. 8, A). *Indumentum.* Cephaloprothorax with more than 5 dorsal setae, enlarged seta near base of clypeus on each side; clypeus without basal setae, abdominal segments with several setae in transverse row extending across central portion of abdomen, most segments with one or more setae clustered near spiracles along abdomen margin. *Antennae* (Figs. 3, C, H). Resembling antennae of second instar except for presence of dorsal sensorium, ventral seta on apical segment. *Legs* (Fig. 4, C). *Circumanal pore rings* (Figs. [8, E]; 15, [A]-D).

FOURTH INSTAR.

Dimensions. Length 2.07-2.67, [2.07-2.67]; width 1.53-1.97, [1.53-1.90].

Dorsum (Fig. 9, A). *Indumentum.* Cephaloprothorax without relatively enlarged dorsal seta on each side. [Lateral margin of abdomen (Fig. 16, M) with admarginal row of spathulate setae; posterior margin of abdomen (Fig. 16, I) with admarginal row of sectasetae].

Venter (Fig. 9, A). *Sclerotization.* Abdominal segment with small sclerotized plate between spiracular plates on each side (not illustrated). *Indumentum.* Cephaloprothorax with 2 enlarged setae near base of clypeus on each side. *Cuticular structures.* Minute point, spinule configuration

resembling third instar (not illustrated). *Antennae* (Figs. 3, D, I). Three segmented; basal segment resembling third instar; second segment with 2 ventral setae, 1 apical, 1 submedial, 1 laterodorsal sensorium near apex; apical segment resembling apical segment of third instar except for presence of 2 setae on venter. *Legs* (Fig. 4, D). Meso-, metafemora with 3 ventral sensoria near base. *Circumanal pore rings* (Figs. [9, F]; 17, [A]-D).

FIFTH INSTAR.

Dimensions. Length 3.40-4.50, [3.40-4.50]; width 2.45-2.90, [2.45-3.35].

Dorsum (Fig. 10, A). *Indumentum.* Cephaloprothorax with 3-4 enlarged setae near anterior end of clypeus on each side. *Antennae* (Figs. 3, E, J). Six segmented; basal segment with ventral seta, dorsal sensorium; second segment with 2 ventral setae, 1 subapical, 1 medial; fourth segment with ventral seta, laterodorsal sensorium; fifth segment with ventral seta; apical segment resembling apical segment of fourth instar. *Legs* (Fig. 4, E). Profemora with 4 ventral sensoria; meso-, metafemora each with 5 ventral sensoria near base (Fig. 10, A).

Venter (Fig. 10, A). *Circumanal pore rings* (Figs. [10, F]; 19, [A]-D).

TYPES

The type series (BISHOP 5532) is labeled Punaluu, Oahu, Coll. O. H. S. This series was described by Crawford from two paratype specimens mounted to one insect pin. The male is here designated as lectotype and female as paralectotype.

Other specimens examined. HAWAII, OAHU I., KOOLAU MTS., POAMOHO TRAIL: 3 males (2 on slides), 3 females (2 on slides), 64 nymphs (4 III, 26 IV, 34 V), 730 m, 21.iv.1979, ex. *Pritchardia* sp., G. K. Uchida and F. G. Howarth; 24 males, 4 females, lab. reared, F₁, G. K. Uchida; 16 males, 10 females, lab. reared, F₂, G. K. Uchida; 1 female, 156 nymphs (17 I, 58 II, 57 III, 24 IV), lab. reared, F₃, G. K. Uchida; 8 males (1 in alcohol), 6 females, 22 nymphs (3 I, 4 II, 5 III, 5 IV, 5 V), 2500', 24.iv.1981, ex. *Pritchardia* sp., G. K. Uchida; 6 males, 1500', 8.iii.1970, ex. *Pritchardia*, W. C. Gagné. OAHU I., KOOLAU MTS.: 4 nymphs (1 I, 1 II, 1 III, 1 IV), Wiliwilinui Tr., 2000', 28.v.1979, ex. *Pritchardia* sp., G. K. Uchida; 1 male, 7 nymphs (2 I, 1 II, 1 III, 1 IV, 2 V), Aiea, Puu Kawaipoo, 7.x.1979, ex. *Pritchardia martii*, G. K. Uchida; 4 males (2 in alcohol), 25 nymphs (1 II, 3 III, 8 IV, 13 V) Castle Tr., 2100', 1.iii.1981, ex. *Pritchardia rockiana*, W. C. Gagné; 4 males in alcohol, 1 female, 17 nymphs (4 I, 7 II, 6 III), Castle Trail, nr. stream, 28.iv.1981, ex. *Pritchardia rockiana*, J. Obata; 5 males, 2 females, Waikane, x-22-1947, E. C. Zimmerman; 1 male, Manoa Valley, x-1947, E. C. Zimmerman; 3 males, 3 females, Mt. Olympus, 1-12-19, O. H. Swezey; 9 males, 6 females, Mt. Olympus, 1.19.19, O. H. Swezey; 1 male, 1 nymph (V), Konahuanui, Jun. 12, 1919, J. C. Bridwell. OAHU I., WAIANAE MTS., MAKALEHA VALLEY: 1 male, 5 nymphs (4 III, 1 V), 22.vii.1979, ex. *Pritchardia kaalae*, G. K. Uchida; 6 nymphs (1 I, 1 II, 1 III, 2 IV, 1 V), 25.v.1980, ex. *Pritchardia kaalae*, G. K. Uchida.

***Megatrioza kauaiensis* Uchida & Beardsley, n. sp.**

(Figs. 5, A-B; 11, B; 12, B, F, J, N; 13, B, F, J, N, R; 14, B, F; 15, B; 16, F, J, N; 17, B; 18, J; 19, B).

ADULT STAGE

Dimensions. Body length - male 2.9, female 3.8; width - male 1.1, female 1.3. Forewing length - male 3.6, female 4.3; width - male 1.3, female 1.6.

Diagnosis. *M. kauaiensis* recognized by somewhat continuous brown longitudinal stripe on each side of vertex, pronotum, prescutum (Fig. 11, B). The capitate aedeagus (Fig. 5, A) differs from spoon-shaped aedeagus (Fig. 5, B) of *M. kauaiensis*.

Holotype. Male. *Color.* General color light brown with brown markings. *Head* (Fig. 11, B). Antennae light brown, segment IV brown distally, V-X brown; vertex with longitudinal brown streak passing through foveal depression, not reaching posterior margin; anterior, dorsal ocelli red; genal cones brown; eyes black; clypeus light brown. *Thorax* (Fig. 11, B). Pronotum with brown margin except medially, longitudinal brown streak submedially on each side; mesothoracic prescutum, scutum with two somewhat longitudinal streaks laterally on each side; mesothoracic scutellum with W-shaped brown mark. *Wings.* Clear; R+M+Cu junction, distal ends of Rs, M₁₊₂, M₃₊₄, Cu_{1a}, Cu_{1b}, A, hind margin adjacent to radular spinules, radular spinules brown. *Legs* light brown with brown markings; pro-, mesofemora with light brown spot distally; metatibiae with light brown genual spine, inner subapical, outer apical saltatorial spines black apically; tarsal segments of pro-, meso-, metatarsi brown. *Abdomen.* Segments brown, intersegmental membrane orange dorsally; proctiger brown anteroapically, parameres brown apically; subgenital plate with lateral brown spot on each side.

Allotype. Female. Fitting description of male except for following characteristics: *Head.* Genal cones light brown; antennae with segment IV distally, V-X brown. *Abdomen.* Proctiger brown anterodorsally.

IMMATURE STAGES

FIRST INSTAR.

Dimensions. Length 0.51-0.53; width 0.29-0.31.

Margin. Flattened spine-like projection (Fig. 12, B) length about 3 times as long as basal width.

Dorsum. Indumentum. Sectasetae (Figs. 12, B, F, J, N) lanceolate. Cephaloprothorax (Fig. 12, F) with 2 greatly enlarged dorsal setae on each side.

Venter. Circumanal pore ring (Fig. 12, N).

SECOND INSTAR.

Dimensions. Length 0.86-0.95, width 0.63-0.71.

Dorsum. Indumentum. Cephaloprothorax (Fig. 13, F), abdomen (Figs. 13, J, N, R) with admarginal row of lanceolate sectasetae; anterior, posterior wingpads (Fig. 13, B) with admarginal row of setae.

Venter. Circumanal pore rings (Fig. 13, R).

THIRD INSTAR.

Dorsum. Indumentum. Cephaloprot thorax (Fig. 14, F), wingpads (Fig. 14, B) with admarginial row of setae, few poorly to well developed setae interspersed on cephaloprot thorax. Cephaloprot thorax, greatly enlarged dorsal seta on each side of cephaloprot thorax.

Ventre. Circumanal pore rings (Fig. 15, B).

Dorsum. Indumentum. Cephaloprot thorax (Fig. 16, F) with setae in ad-

Dorsum. Indumentum. Cephaloprot thorax (Fig. 16, J) with setae in ad-

Dorsum. Indumentum. Cephaloprot thorax (Fig. 16, N) may be present anteriorly on each side.

Ventre. Circumanal pore rings (Fig. 17, B).

Dorsum. Indumentum. Abdomen (Fig. 18, J) with setae close in 3 closely spaced submarginal rows, outer row admarginial.

Dorsum. Indumentum. Abdomen (Fig. 19, B).

Dorsum. Indumentum. Abdomen (Fig. 19, V), 3 eggs, same locality data as holotype; 1 male abdomen

Paratypes, 5 males (2 in alcohol), 2 females (1 in alcohol), 19 nymphs (3 I, 2 II, 4 III, 4 IV, 6 V), 1 female, 9 nymphs (1 II, 3 III, 3 IV, 2 V), 20000, 10.VI.1981, ex.

*Holotype male, allotype female, Hawaii, Kauai I., Power Line Rd., 575 m., 19.VII.1981, ex. *Prichardia hardyi* (C. K., Uchida (BISHOP 13589).*

Types (Figs. 5, A-B; 11, C; 12, C, G, K, O; 13, C, G, K, O, S; 14, C, G; 15, C; 16,

Megaritiza molokaiensis Uchida & Beardsley, n. sp.

ADULT STAGE

C, K, O; 17, C; 18, C, G; 19, C).

Dimensions. Body length - male 2.6, female 3.5; width - male 1.1, female

1.2. Forewing length - male 3.3, female 4.3; width - male 1.2, female 1.6.

Headshape. Male, Color. General color light brown with dark brown

*shaped adeagus (Fig. 5, B) of *M. hanaiensis*.*

Diagnostics. M. molokaiensis with light brown median stripe mainly on scutum. The capitate adeagus (Fig. 5, A) differs from me-

brown streak on each side of prescutum; brown longitudinal stripe by

anterior margin, foreal depressions lighter brown, pale orange centrally;

posterior margin, foreal depressions darker brown along anterior,

dark brown, V, VI lighter brown; vertex dark brown along male I, IX, X

markings. Head (Fig. 11, C). Antennae light brown, segments I, II, III, X

dark brown, dorsal ocelli red; genal cones dark brown; eyes black; clypeus

brown. Thorax (Fig. 11, C). Pronotum with dark brown margin, dark

brown stripe anterior, dorsal ocelli red; genal cones dark brown; eyes black;

posterior margin, foreal depressions lighter brown, pale orange centrally;

posterior margin, foreal depressions darker brown along male I, II, III, X

markings. Head (Fig. 11, C). Antennae light brown, segments I, II, III, X

dark brown, V, VI lighter brown; vertex dark brown, pale orange centrally;

posterior margin, foreal depressions darker brown along male I, II, III, X

markings. Head (Fig. 11, C). Antennae light brown, segments I, II, III, X

dark brown, V, VI lighter brown; vertex dark brown, pale orange centrally;

posterior margin, foreal depressions darker brown along male I, II, III, X

markings. Head (Fig. 11, C). Antennae light brown, segments I, II, III, X

dark brown, V, VI lighter brown; vertex dark brown, pale orange centrally;

posterior margin, foreal depressions darker brown along male I, II, III, X

markings. Head (Fig. 11, C). Antennae light brown, segments I, II, III, X

dark brown, V, VI lighter brown; vertex dark brown, pale orange centrally;

posterior margin, foreal depressions darker brown along male I, II, III, X

markings. Head (Fig. 11, C). Antennae light brown, segments I, II, III, X

dark brown, V, VI lighter brown; vertex dark brown, pale orange centrally;

posterior margin, foreal depressions darker brown along male I, II, III, X

markings. Head (Fig. 11, C). Antennae light brown, segments I, II, III, X

dark brown, V, VI lighter brown; vertex dark brown, pale orange centrally;

posterior margin, foreal depressions darker brown along male I, II, III, X

markings. Head (Fig. 11, C). Antennae light brown, segments I, II, III, X

dark brown, V, VI lighter brown; vertex dark brown, pale orange centrally;

posterior margin, foreal depressions darker brown along male I, II, III, X

markings. Head (Fig. 11, C). Antennae light brown, segments I, II, III, X

dark brown, V, VI lighter brown; vertex dark brown, pale orange centrally;

posterior margin, foreal depressions darker brown along male I, II, III, X

markings. Head (Fig. 11, C). Antennae light brown, segments I, II, III, X

dark brown, V, VI lighter brown; vertex dark brown, pale orange centrally;

posterior margin, foreal depressions darker brown along male I, II, III, X

markings. Head (Fig. 11, C). Antennae light brown, segments I, II, III, X

dark brown, V, VI lighter brown; vertex dark brown, pale orange centrally;

posterior margin, foreal depressions darker brown along male I, II, III, X

markings. Head (Fig. 11, C). Antennae light brown, segments I, II, III, X

dark brown, V, VI lighter brown; vertex dark brown, pale orange centrally;

lighter brown streak on each side, dark brown laterally; mesothoracic scutellum with W-shaped dark brown mark; metathoracic pleura, sternum brown. *Wings.* Clear; basal 1/3 with oblique smoky brown streak on distal ends of c+sc, clavus; R+M+Cu, R, Cu, Cu_{1b}, bases of C+Sc, R, Rs, M, Cu_{1a}, A distally, hind margin adjacent radular spinules, radular spinules dark brown. *Legs.* Light brown with brown markings; metafemora with brown longitudinal streak dorsally, brown band apically; metatibiae with brown genual spine, inner subapical, outer apical saltatorial spines black apically; pro-, meso-, metatarsi brown apically. *Abdomen.* Dark brown; intersegmental membrane orange dorsally; proctiger dark brown anteriorly; parameres dark brown apically.

Allotype. Female. Fitting description of male except for following characteristics:

Abdomen. Proctiger, subgenital plate dark brown.

IMMATURE STAGES

FIRST INSTAR.

Dimensions. Length 0.54-0.56, width 0.32-0.33.

Margin. Flattened spine-like projection (Fig. 12, C) length about 2 times as long as basal width.

Dorsum. Indumentum. Cephaloprothorax (Figs. 12, G) with narrowly lanceolate sectasetae, distal section of sectasetae nearly linear, with 2-3 greatly enlarged dorsal setae on each side.

Venter. Circumanal pore ring (Fig. 12, O).

SECOND INSTAR.

Dimensions. Length 0.89-0.94, width 0.61-0.68.

Dorsum. Indumentum. Cephaloprothorax (Fig. 13, G) with narrowly lanceolate sectasetae with distal section nearly linear; wingpads (Fig. 13, C), abdomen (Figs. 13, K, O, S), with admarginal row of lanceolate sectasetae. Greatly enlarged submarginal seta on each side of cephaloprothorax.

Venter. Circumanal pore rings (Fig. 13, S).

THIRD INSTAR.

Dimensions. Length 1.50, width 1.17.

Dorsum. Indumentum. Cephaloprothorax (Fig. 14, G) with setae in admarginal row, mixed with poorly developed sectasetae; anterior wingpads (Fig. 14, C) with admarginal row of setae mixed with sectasetae posteriorly; posterior wing pads (Fig. 14, C) with admarginal row of setae mixed with sectasetae.

Venter. Circumanal pore rings (Fig. 15, C).

FOURTH INSTAR.

Dimensions. Length 2.10-2.47, width 1.57-1.90.

Dorsum. Indumentum. Setae in admarginal row on anterior wingpads (Fig. 16, C), posterior wing pads (Fig. 16, C), mixed with sectasetae posteriorly on posterior wingpads; abdomen with sectasetae in 2 closely spaced submarginal rows (Fig. 16, K), outer row admarginal, 1 to few admarginal setae anteriorly on each side (Fig. 16, O).

Venter. Circumanal pore rings (Fig. 17, C).

FIFTH INSTAR.

Dimensions. Length 3.40-3.95, width 2.60-3.00.

Dorsum. Indumentum. Setae in admarginal row on cephaloprothorax (Fig. 18, G), wingpads (Fig. 18, C).

Venter. Circumanal pore rings (Fig. 19, C).

TYPES

Holotype male, allotype female, Hawaii, Molokai I., above Waialeia, Kahanui Ridge, 750 m., 28.xii.1981, ex. *Pritchardia* sp., G. K. Uchida and L. Mollena (BISHOP 13590). Paratypes. 5 males (4 in alcohol), 5 females (2 in alcohol), 13 nymphs (4 I, 7 II, 1 IV, 1 V), same locality data as holotype, 5 males, 4 females, 12 nymphs (1 II, 1 III, 7 IV, 3 V), same locality data as holotype, lab. reared, F1.

***Megatrioza mauiensis* Uchida & Beardsley, n. sp.**

(Figs. 5, A-B; 11, D; 12, D, H, L, P; 13, D, H, L, P, T; 14, D, H; 15, D; 16, D, H, L; 17, D; 18, L; 19, D).

ADULT STAGE

Dimensions. Body length - male 2.9, female 3.6; width - male 1.2, female 1.5. Forewing length - male 4.0, female 4.8; width - male 1.5, female 1.9.

Diagnosis. *M. mauiensis* (Fig. 11, D) recognized by dark brown vertex of head; medial stripe on prescutum; scutum with brown submedial spot on each side. The capitate aedeagus (Fig. 5, A) differs from spoon-shaped aedeagus (Fig. 5, B) of *M. kauaiensis*.

Holotype. Male. *Color.* General color light brown with dark brown markings. *Head* (Fig. 11, D). Antennae brown, segments I, II, IX, X dark brown; vertex dark brown; anterior, dorsal ocelli red; genal cones dark brown; eyes black; clypeus dark brown. *Thorax* (Fig. 11, D). Pronotum brown, dark medially; mesothoracic prescutum dark brown, submedial brown spot on each side; mesothoracic scutum with wide dark brown stripe medially, flanked by dark brown streak laterally on each side; mesothoracic scutellum with W-shaped dark brown mark; mesothoracic pleura, sternum dark brown. *Wings* clear; c+sc, clavus almost entirely smoky brown; R+M+Cu, R, Cu₁, Cu_{1b}, Cu₂, bases of C+Sc, Rs, M, Cu_{1a}, A-hind margin break, hind margin adjacent radular spinules, radular spinules brown. *Legs* light brown; metafemora with brown streaks laterally on each side; metatibiae with brown genual spine, inner subapical, outer apical saltatorial spines black apically; basal segment of pro-, meso-, metatarsi brown distally, apical segments brown. *Abdomen* dark brown, intersegmental membrane orange dorsally; proctiger, parameres dark brown.

Allotype. Female fitting description of male except for following characteristics:

Abdomen. Proctiger, subgenital plate dark brown.

IMMATURE STAGES

FIRST INSTAR.

Dimensions. Length 0.57; width 0.33-0.34.

Margin. Flattened spine-like (Fig. 12, D) projection length about as long as basal width.

Dorsum. Sectasetae lanceolate (Figs. 12, D, H, L, P). Cephaloprothorax (Fig. 12, H) with greatly enlarged dorsal seta on each side.

Venter. Circumanal pore ring (Fig. 12, P).

SECOND INSTAR.

Dimensions. Length 0.90-0.96; width 0.63-0.68.

Dorsum. Indumentum. Body (Figs. 13, D, H, L, P, T) with lanceolate sectasetae in admarginal row. Dorsal setae reduced in size; cephaloprothorax (Fig. 13, H) with relatively enlarged dorsal seta with enlarged base on each side.

Venter. Circumanal pore rings (Fig. 13, T).

THIRD INSTAR.

Dimensions. Length 1.42-1.55; width 1.03-1.15.

Dorsum. Indumentum. Setae in admarginal row on cephaloprothorax (Fig. 14, H), anterior wingpads (Fig. 14, D); setae mixed with sectasetae on posterior wingpads (Fig. 14, D).

Venter. Circumanal pore rings (Fig. 15, D).

FOURTH INSTAR.

Dimensions. Length 2.40-2.53; width 1.80-1.90.

Dorsum. Indumentum. Posterior wingpads (Fig. 16, D) with simple setae in admarginal row; abdomen (Figs. 16, L; 17, D) with sectasetae in 2 closely placed submarginal rows, outer row admarginal; 1 to few admarginal setae may be present anteriorly on each side.

Venter. Circumanal pore rings (Fig. 17, D).

FIFTH INSTAR.

Dimensions. Length 3.50-4.20; width 2.65-3.20.

Dorsum. Abdomen (Fig. 18, L) with sectasetae in 3 closely placed submarginal rows, outer row admarginal.

Venter. Circumanal pore rings (Fig. 19, D).

TYPES

Holotype male, allotype female (tip of right wing missing), Hawaii, Maui I., nr. Lanilili, 670 m., 3.x.1981, ex. *Pritchardia* sp., G. K. Uchida (BISHOP 13588). Paratypes. Nine males (2 in alcohol), 3 females (2 in alcohol), 31 nymphs (4 I, 6 II, 6 III, 6 IV, 9 V), same locality data as holotype.

BIOLOGY

The species of the *M. palmicola* group collected from the major Hawaiian Islands of Kauai, Oahu, Molokai and Maui were found to be restricted to elevations above 425 m on native fan palms, *Pritchardia* spp.

The nymphs of *Megatrioza* displayed a negative phototropic response and usually resided in the narrow folds of young leaves and narrow spaces

of the axils of the upper whorl of older expanded leaves of *Pritchardia*. Apparently, temperature and humidity may have a great influence on the survival of these psyllids. In the field, *Pritchardia* spp. are usually restricted to the cloud zone or in areas which are frequently subjected to inundation by fog. Thus, the confined areas of refuge for the psyllid nymphs on the palm trees frequently contained a film of water through which the nymphs moved about. At 69% relative humidity laboratory reared nymphs in screen cages survived much better when they fed at the base of the palm seedling near the moist potting soil than nymphs which fed on the more exposed juvenile leaves. Nymphs reared under higher humidity conditions of 80% survived even on the exposed juvenile leaves of the palm seedling. Temperature may be another important factor influencing survival because, in their natural environment, *Megatrioza* are exposed to temperatures cooler than those which occurred in the laboratory. However, this supposition requires further testing.

Observations on the biology of *Megatrioza* were made for *M. palmicola* (Oahu Island), *M. kauaiensis* (Kauai Island) and *M. mauiensis* (Maui Island). Adults of *Megatrioza* spp. were inactive in the field during the sunny periods of the day. Studies by Baldwin (1953) and S. L. Montgomery (pers. comm.) on the stomach contents of 3 native honey creepers (*Vestiaria coccinea*, *Himatione sanguinea* and *Loxops virens*) indicated that the *Trioza* on the host plant 'ohi'a (*Metrosideros collina polymorpha*) were one of the major kinds of insect food for these birds. The negative phototropic response to light by nymphs and behavior of adults in remaining inactive on the under side of the leaves of *Pritchardia* during sunny periods may be a selective advantage against predation by birds as well as by other diurnal arthropod predators.

The courtship and mating behavior of *Megatrioza* have not been observed in the field on its host plant. However, *M. palmicola* adults were very active on *Pritchardia martii* on Poamoho Trail, Oahu Island one hour prior to sunset under heavy cloud cover. The adults were apparently in the process of courting. Captive adults of both sexes of *Megatrioza* spp., transported in vials, were frequently found to be *in copula*. Low light intensity was necessary to initiate courtship and mating behavior in both the field and laboratory.

The courtship behavior of adult *Megatrioza* was relatively simple. The male of *M. palmicola* appeared to hold the posterior edges of its forewings in contact (as if to hinge on one another) over the abdomen and by raising and dropping the anterior edges vertically, the male fluttered its wings in 2 sets for an undetermined number of beats per set. The wings were then returned to its rest position. The male performed this behavior several times prior to copulation. The female's response was not observed.

The courtship behavior of *M. kauaiensis* male was similar except that the male fluttered its wings in 3 sets for an undetermined number of beats per set and at intervals of 2.5 to 3.0 sec between sets, with the female usually responding immediately with an apparently single beat.

M. mauiensis differed from *M. kauaiensis* in that the female gave a delayed response each time the male beat its wings.

The males of *M. kauaiensis* and *M. mauiensis* fluttered their wings several times before attempting to copulate. The females usually walked away from advancing males. The males usually approached the females from the right side with wings held horizontally over its abdomen. Copulating males rested the forewing which was closest to the female on top of the female's forewings. A mating pair of *M. kauaiensis* remained *in copula* for 1 hr. 29 min. and *M. mauiensis* for 1 hr. 35 min.

No attempt was made to determine if the fluttering of the wings produced sound by means of vibration or stridulation (Taylor, 1985).

Three days after mating, the females of *M. kauaiensis* and *M. mauiensis* began laying eggs on seedlings of *Pritchardia*. Females of *M. kauaiensis* walked quickly up and down the seedling and stopped at frequent intervals along the longitudinal axis of the leaf veins and petioles to lay a line of eggs. The thorax was held further away from the leaf surface than when at rest, with the abdomen arched posteriorly. Each time a female stopped, it swayed its body backwards, apparently inserting an egg with its ovipositor into the veins of the leaf. Eggs were deposited singly or in rows, with each egg about 0.5 mm apart. The tendency of most females was to deposit eggs in the narrow folds of the young leaves of the palm seedlings. Field collected eggs were found to be embedded in the scaly surface of veins of young leaves of mature palms. A single captive female oviposited 83 eggs.

Females of *M. mauiensis* assumed the same posture as those of *M. kauaiensis* during egg laying, but moved more slowly. This behavior was also observed in the field when blanketed by clouds. During sunny periods of the afternoon, adults remained inactive on the underside of leaves. Laboratory reared females oviposited preferentially in rows on the veins of folded leaves. Eggs were deposited very close to each other, almost in contact. On Maui, eggs were found on the veins of both expanded, and, folded leaves of mature palms. Viable eggs were not found on expanded leaves on other islands. One female oviposited 111 eggs in the laboratory.

Hatching of *M. kauaiensis* and *M. mauiensis* was observed 3 days after oviposition. It began when the nymph inside the egg arched dorsally (Fig. 20, A) causing the apex to bulge near an inverted U-shaped line of weakness. The nymph changed its posture by arching ventrally then dorsally and this movement continued until the chorion broke. The nymph, was encased within an epembryonic membrane, slid out of the chorion and arched dorsoventrally in a continuous motion until 3/4 of the body protruded. This caused the epembryonic membrane to rupture and exposed the cephalothorax (Fig. 20, B). The margin of the ruptured end of the epembryonic membrane consisted of a circular row of thread-like projections. Minute teeth were observed on the epembryonic membrane of the egg of *Psylla mali* (Awati, 1915). The epembryonic membrane retracted into the chorion and exposed 3/4 of the nymph (Fig. 20, C).

During this time, the nymph, which prior to eclosion, had assumed the shape of the chorion, expanded to take its own shape. The nymph then arched forward toward the leaf surface and crawled away, freeing its abdomen and stylets. It then stopped and ejected fluid from its anus. The mouth parts were retracted within 5 min after hatching. Nymphs crawled away from direct light to feed and after 24 to 48 hours, they were observed with wax filaments extruded from their sectasetae.

In the field, all 5 nymphal instars of *Megatrioza* spp. can normally be found in the narrow slit-like openings of the young folded leaves of *Pritchardia*. However, the last 3 instars, and rarely the second instar, can also be found in the axils of the upper whorl of leaves. The axils of older leaves contain organic matter and are unsuitable.

Nymphs always fed on the lamina and petiole of the leaves, not on the major veins. They were sedentary and remained in one place for several days. However, occasional movement was observed in the field and laboratory. The exact mode of feeding was not determined, but feeding nymphs would occasionally raise their abdomens with their cephalothorax tilted downward and rotated their bodies, which probably facilitated the movement of their stylets. After feeding, a hole was observed, but no other damage was evident.

Prior to molting, nymphs moved to more exposed areas on the host plant. It was not uncommon to find fifth instar exuviae attached to the underside of the expanded palm leaves, indicating that this was the site of adult emergence. In the laboratory teneral adults remained close to the site of emergence for 24 hr., becoming fully pigmented within 2 days.

DISCUSSION

Origin of Hawaiian *Megatrioza*

The Hawaiian group of *Megatrioza* probably speciated allopatrically. The species which gave rise to the present day *M. palmicola* group has not been found. Crawford (1918) speculated that the progenitor of *M. palmicola* was an early arrival unrelated to other Hawaiian psyllids. Zimmerman (1948) considered *Megatrioza* as an off-shoot of the Hawaiian *Trioza* or South Pacific *Megatrioza*.

Zimmerman's notion that the Hawaiian *Megatrioza* is an offshoot of the Hawaiian *Trioza* can be supported. Apparently, *Pritchardia* has been in the Hawaiian Islands for a long time. Its distribution includes the Northwestern Hawaiian Island of Nihoa and the major islands of Niihau, Kauai, Oahu, Molokai, Maui and Hawaii. Furthermore, an extinct species of a *Pritchardia*-like palm is known to have occurred on the Northwestern Hawaiian island of Laysan. It seems likely that there was sufficient geologic time and opportunity for the *M. palmicola* group to evolve from *Trioza*. However, Zimmerman's alternative hypothesis that the Hawaiian group was derived from South Pacific *Megatrioza* is also logical. *Pritchardia*

spp. are also known from the islands of Fiji, Tonga and the Tuamotu Islands (Hodel, 1980). However, *Megatrioza* needs to be collected from *Pritchardia* in the South Pacific to support this hypothesis.

Speciation of *Megatrioza palmicola* Group

The Hawaiian Archipelago extends in a northwest to a southeast direction for 1,600 mi (Stearns, 1985). The islands in the northwest are small reefs and shoals comprising the tops of old eroded islands, and become progressively younger towards the southern end where the high volcanic islands are found. The ancestor of the *M. palmicola* group probably derived from a vagile founder which colonized the once high islands of the Hawaiian Chain to the Northwest of Kauai, such as Laysan or Nihoa on *Pritchardia* or on some other plant species. Through time, the species of the *M. palmicola* group evolved on *Pritchardia* as monoisland endemics. This apparent lack of adaptive radiation on the host plant has been accompanied by some minor behavioral and morphological differentiation in the adults and nymphs of these geographically isolated taxa. These morphological characteristics have been useful in separating the species.

The *M. palmicola* group has two distinct lines. One, referred to as the *palmicola* line is represented by *M. palmicola*, has immatures possessing stout setasetae and spatulate setae on admarginal regions of the body. The other, the *kauaiensis* line is represented by *M. kauaiensis*, *M. mohokaiensis* and *M. mauiensis*. The immatures possess lanceolate sectasetae and simple setae on admarginal and submarginal regions of the body.

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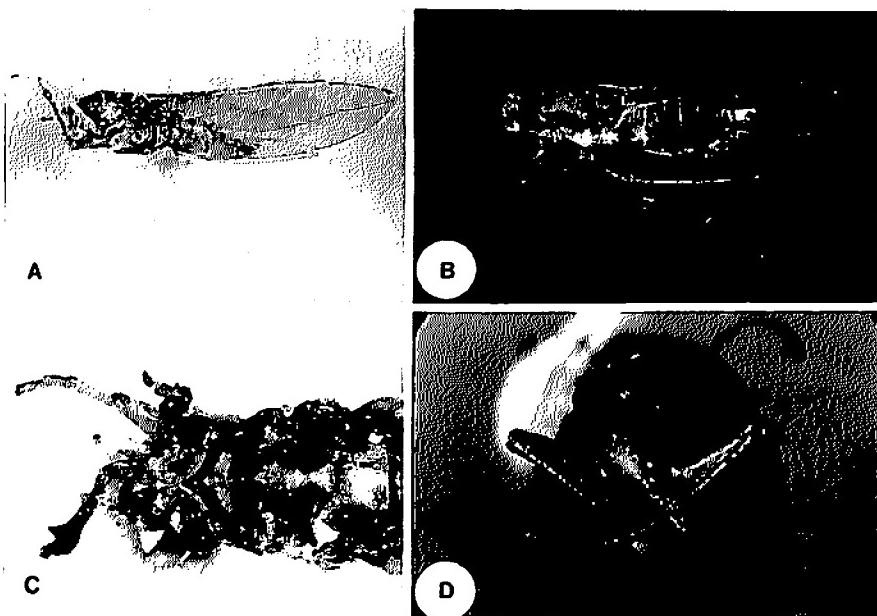


FIGURE 1. (A-B). Lateral aspect. (A) *Megatrioza armata*. (B) *Megatrioza palmicola*. (C) Dorsal aspect of head and thorax of *M. armata*. (D) Anterior aspect of head of *M. palmicola*.

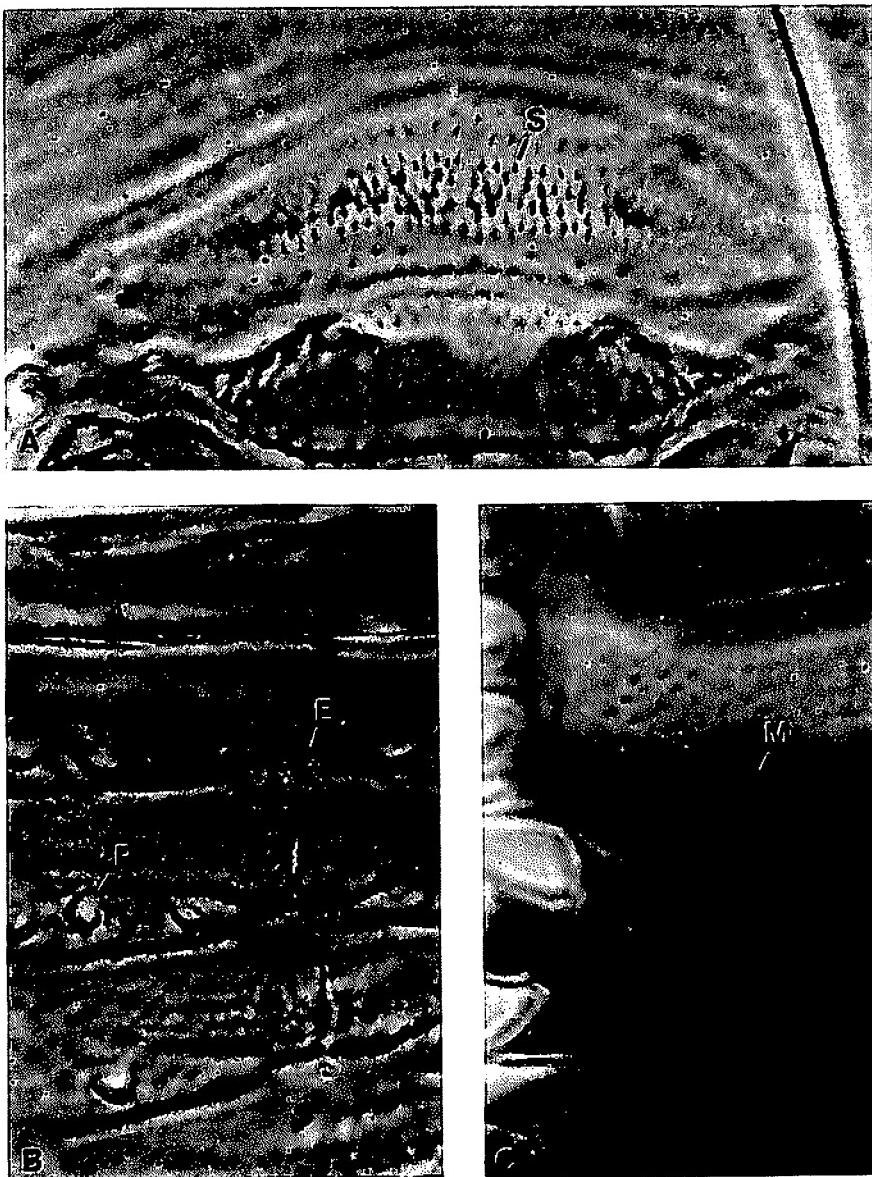


FIGURE 2. *Megatrioza mauiensis*. (A) Ventral aspect of abdomen. S, spinules. (B) Dorsal aspect of abdomen. P, convex, blister-like protuberances; E, subelliptical structure. (C) Ventral aspect of thorax. M, minute points.

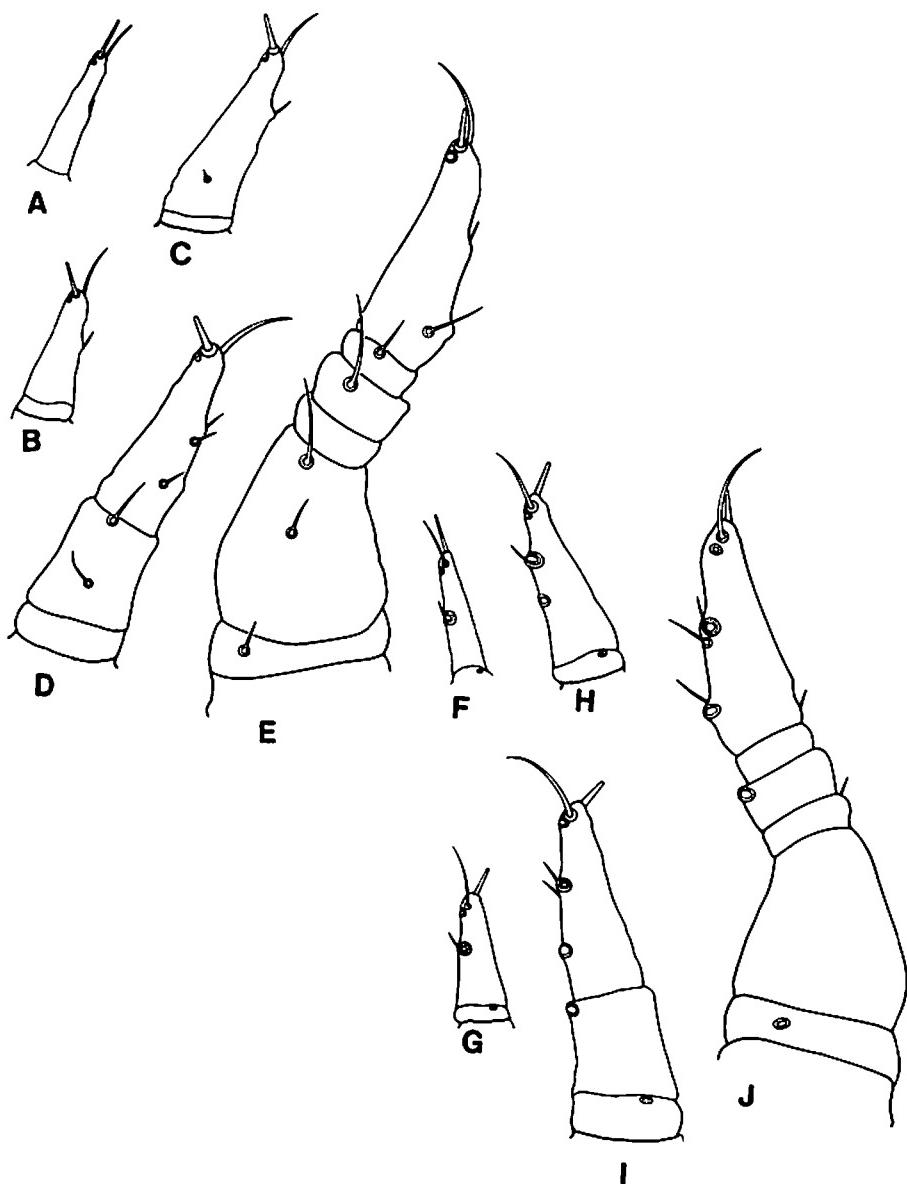


FIGURE 3. Antennae of *Megatriozus palmicola* group. (A-E) Ventral aspect. (A) First instar. (B) Second instar. (C) Third instar. (D) Fourth instar. (E) Fifth instar. (F-J) Dorsal aspect. (F) First instar. (G) Second instar. (H) Third instar. (I) Fourth instar. (J) Fifth instar.

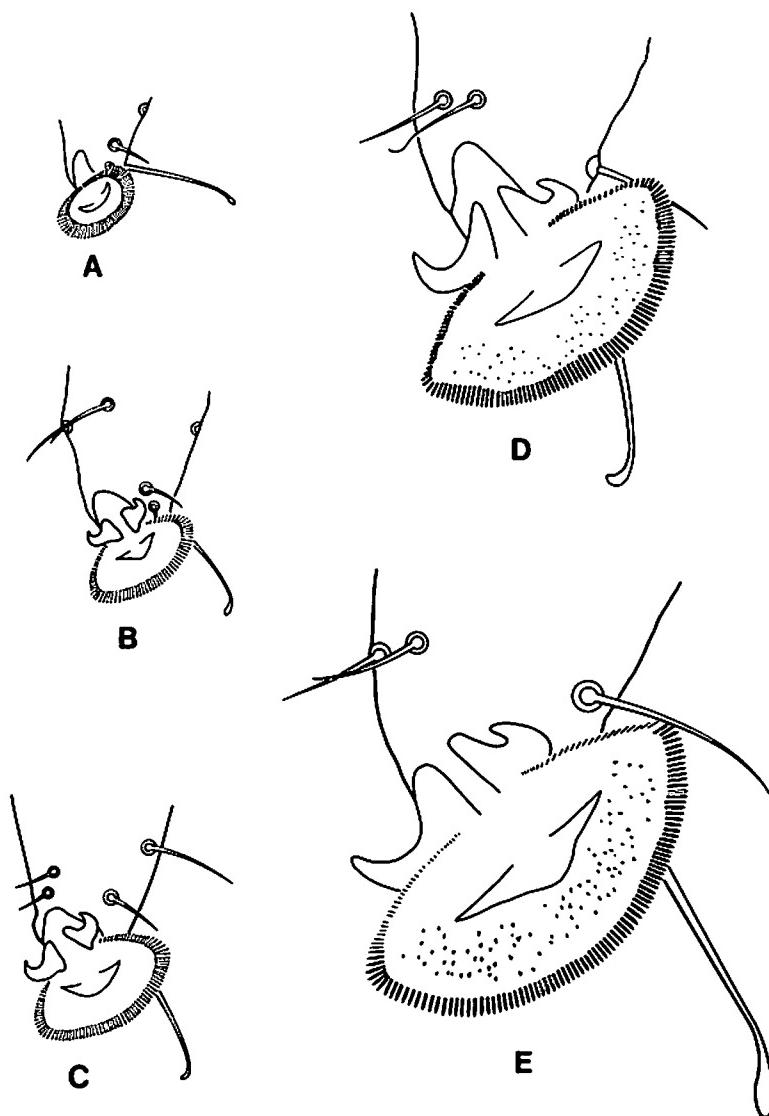


FIGURE 4. Ventral aspect of the apex of tibiotarsus of *Megatrioza palmicola* group. (A) First instar. (B) Second instar. (C) Third instar. (D) Fourth instar. (E) Fifth instar.

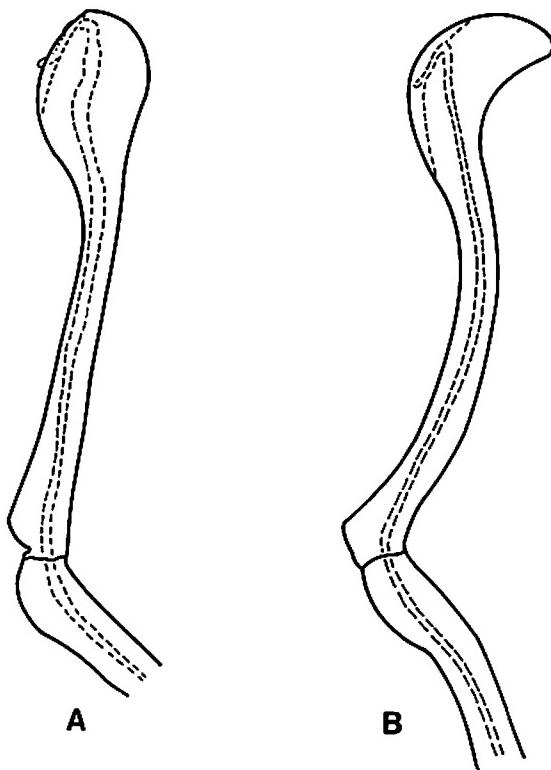


FIGURE 5. Lateral aspect of the aedeagus of *Megatrioz a palmicola* group. (A) *M. palmicola*. (B) *M. kauaiensis*.

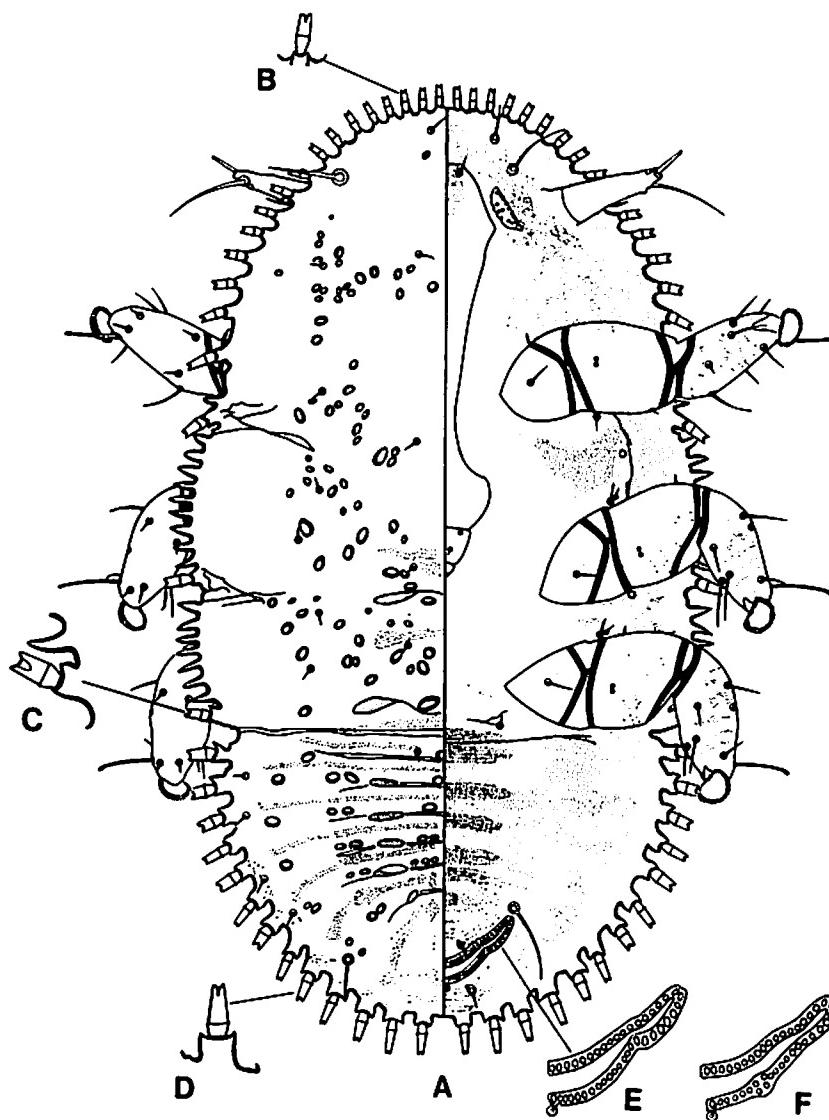


FIGURE 6. First instar of *Megatrioza palmicola*. (A) Dorsal and ventral aspects. (B) Admarginal setaseta on cephaloprothorax. (C) Admarginal setaseta with flattened spine-like projection on metathorax. (D) Admarginal setaseta on abdomen. (E-F) Variation in circummanal pore rings.

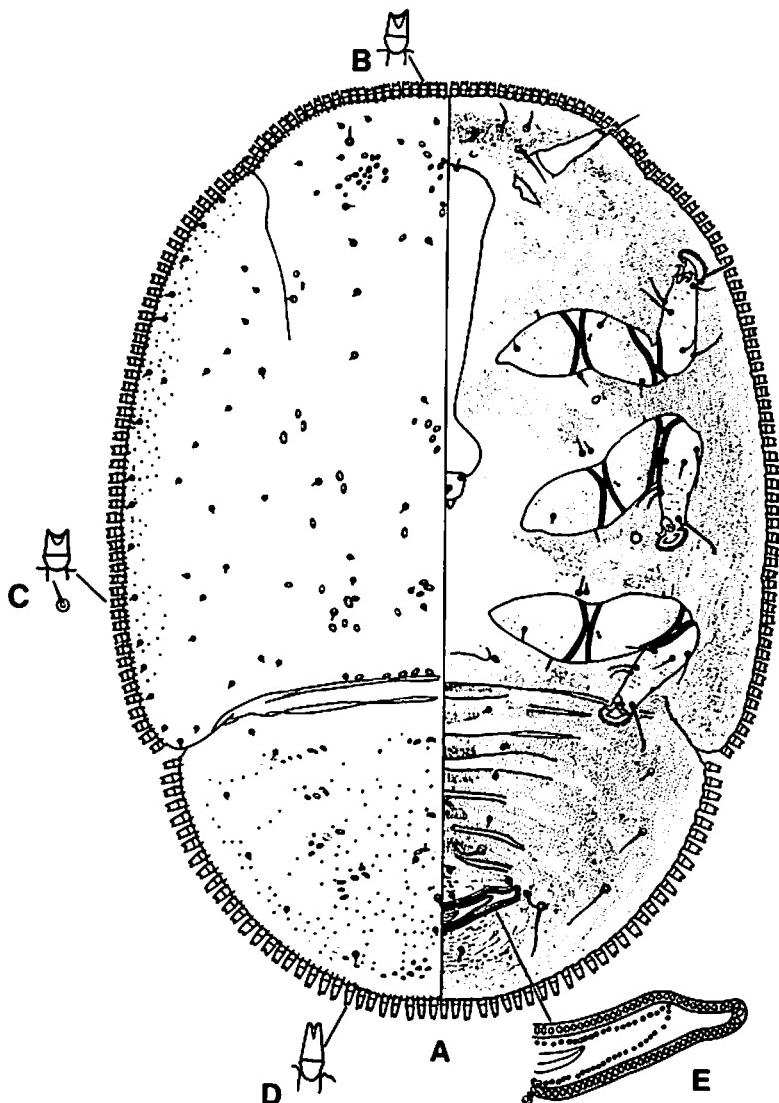


FIGURE 7. Second instar of *Megatrioza palmicola*. (A) Dorsal and ventral aspects. (B) Admarginal sectaseta on cephaloprothorax. (C) Admarginal sectaseta on posterior wingpad. (D) Admarginal sectaseta on abdomen. (E) Circumanal pore rings.

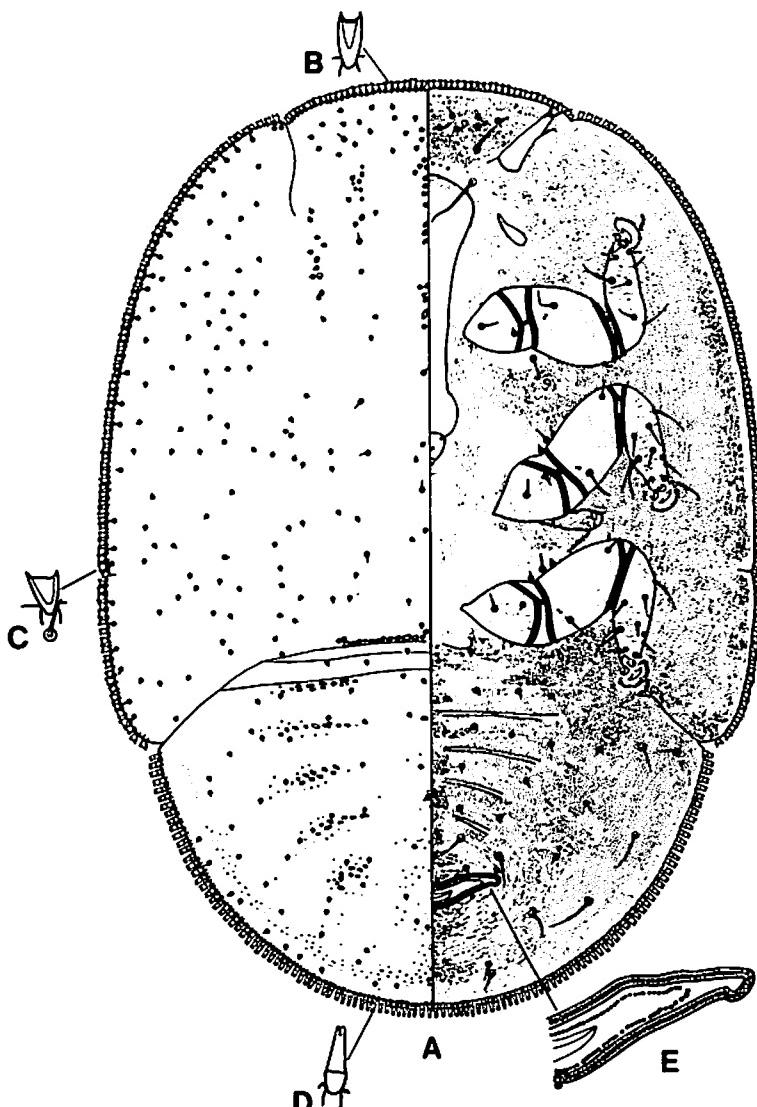


FIGURE 8. Third instar of *Megatrioza palmicola*. (A) Dorsal and ventral aspects. (B) Admarginal setaseta on cephaloprothorax. (C) Admarginal setaseta on anterior wingpad. (D) Admarginal setaseta on abdomen. (E) Circumanal pore rings.

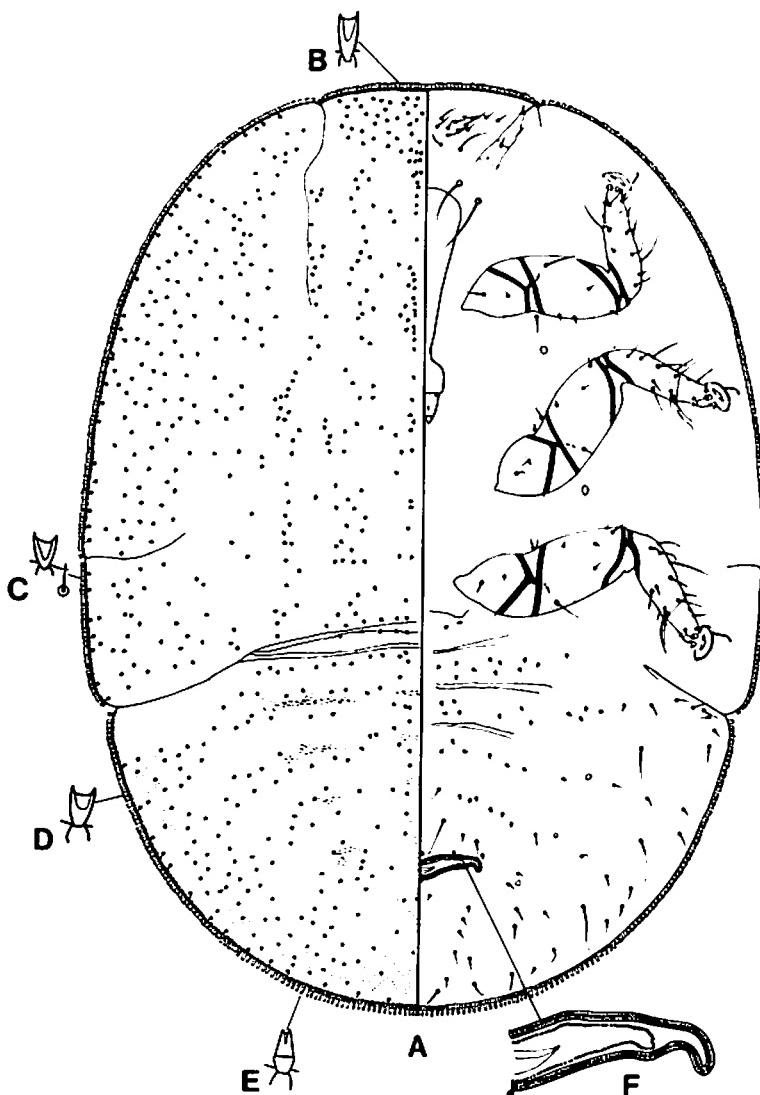


FIGURE 9. Fourth instar of *Megatriozus palmicola*. (A) Dorsal and ventral aspects. (B) Admarginal spathulate seta on cephaloprothorax. (C) Admarginal spathulate seta on posterior wingpad. (D) Admarginal spathulate seta on abdomen laterally. (E) Admarginal sectaseta on abdomen posteriorly. (F) Circumanal pore rings.

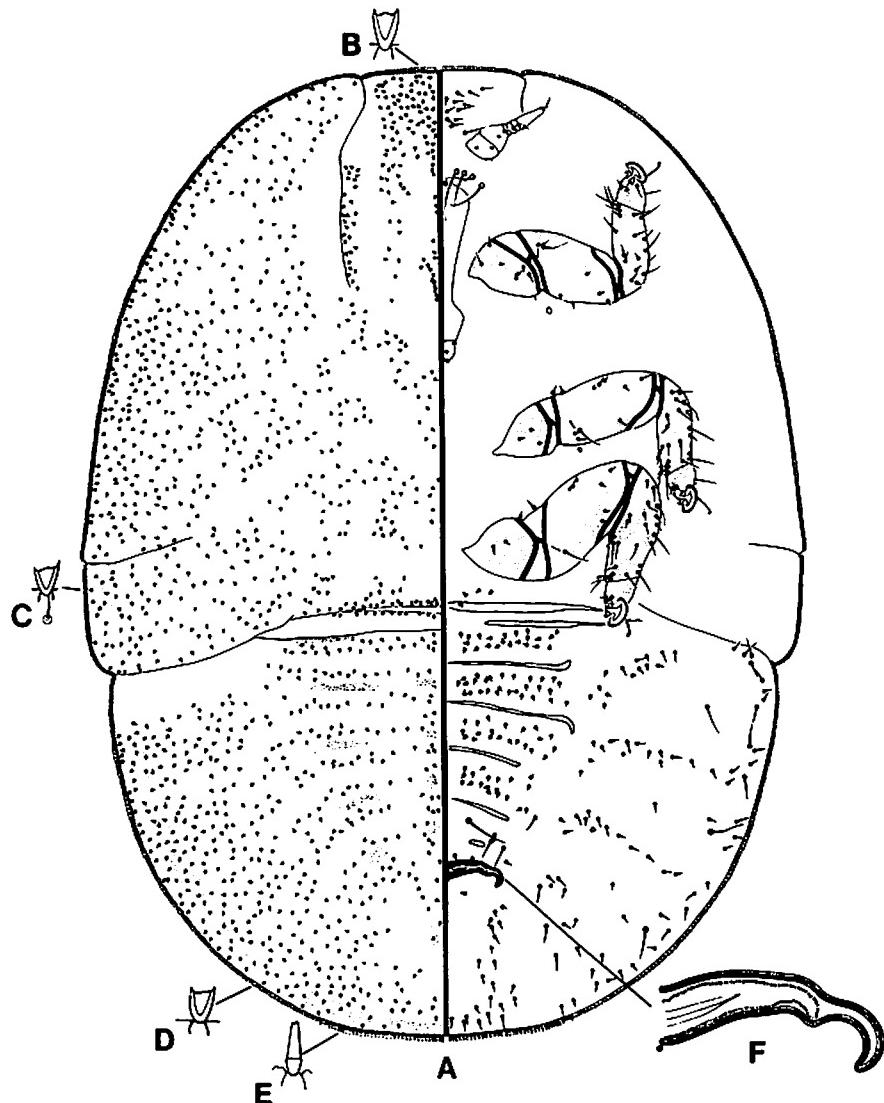


FIGURE 10. Fifth instar of *Megatriozus palmicola*. (A) Dorsal and ventral aspects. (B) Admarginal spathulate seta on cephaloprothorax. (C) Admarginal spathulate seta on posterior wing pad. (D) Admarginal spathulate seta on abdomen laterally. (E) Admarginal sectaseta on abdomen posteriorly. (F) Circumanal pore rings.

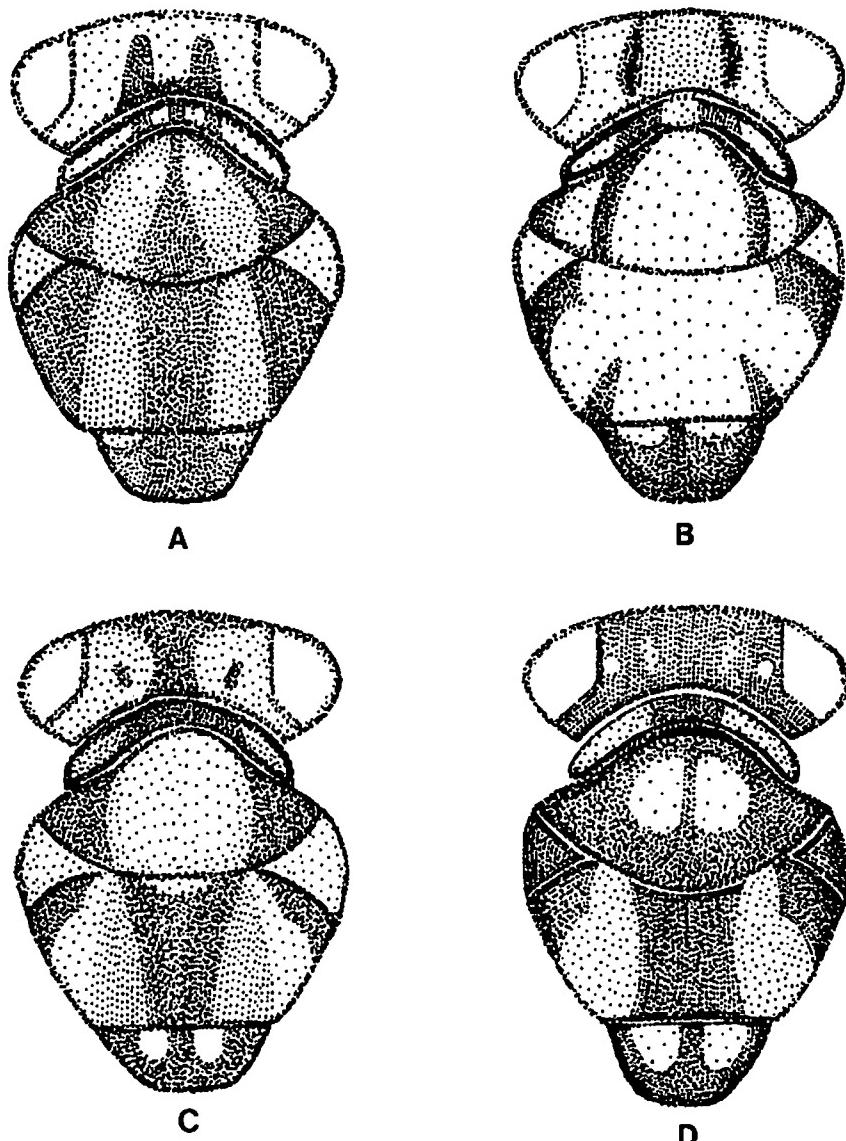


FIGURE 11. Markings on head and thorax of adults of *Megatrioza palmicola* group. (A) *M. palmicola*. (B) *M. kauaiensis*. (C) *M. molokaiensis*. (D) *M. mauiensis*.

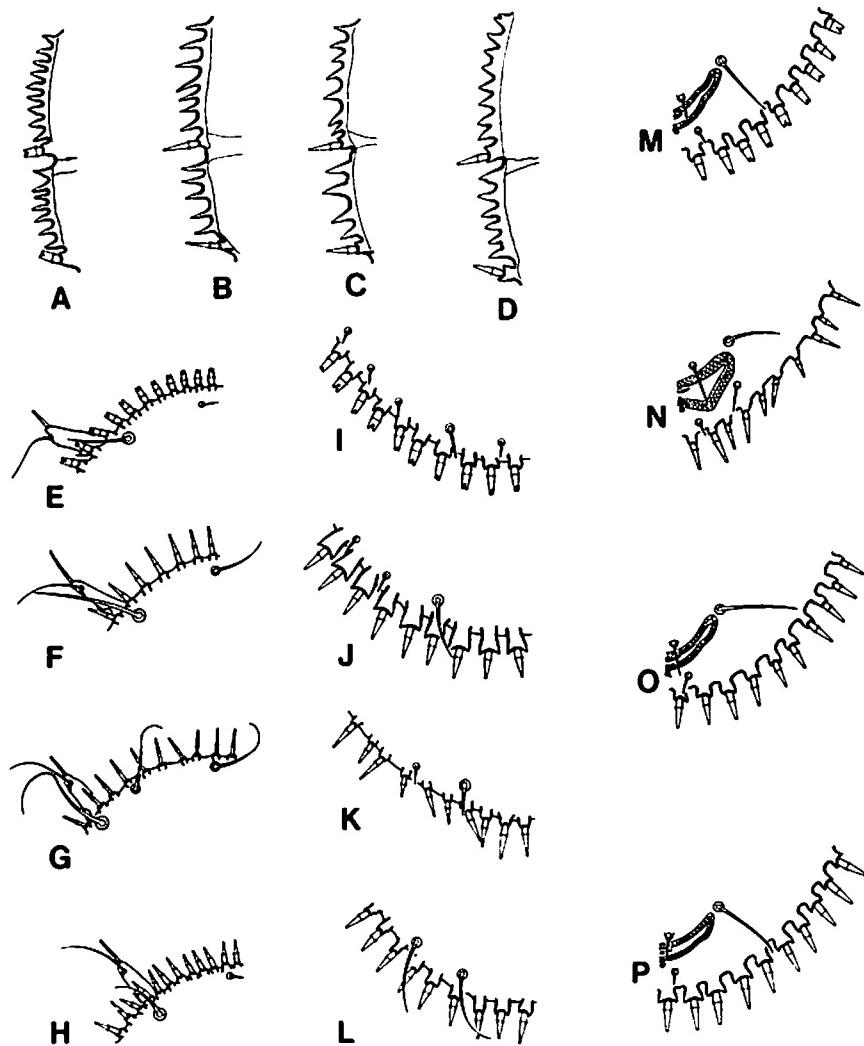


FIGURE 12. First instar nymph of *Megatrioza palmicola* group. (A-D) Dorsal aspect of meso- and metathorax. (A) *M. palmicola*. (B) *M. kauaiensis*. (C) *M. molokaiensis*. (D) *M. mauiensis*. (E-H) Dorsal aspect of cephaloprothorax. (E) *M. palmicola*. (F) *M. kauaiensis*. (G) *M. molokaiensis*. (H) *M. mauiensis*. (I-L) Dorsal aspect of abdomen. (I) *M. palmicola*. (J) *M. kauaiensis*. (K) *M. molokaiensis*. (L) *M. mauiensis*. (M-P) Ventral aspect of abdomen. (M) *M. palmicola*. (N) *M. kauaiensis*. (O) *M. molokaiensis*. (P) *M. mauiensis*.

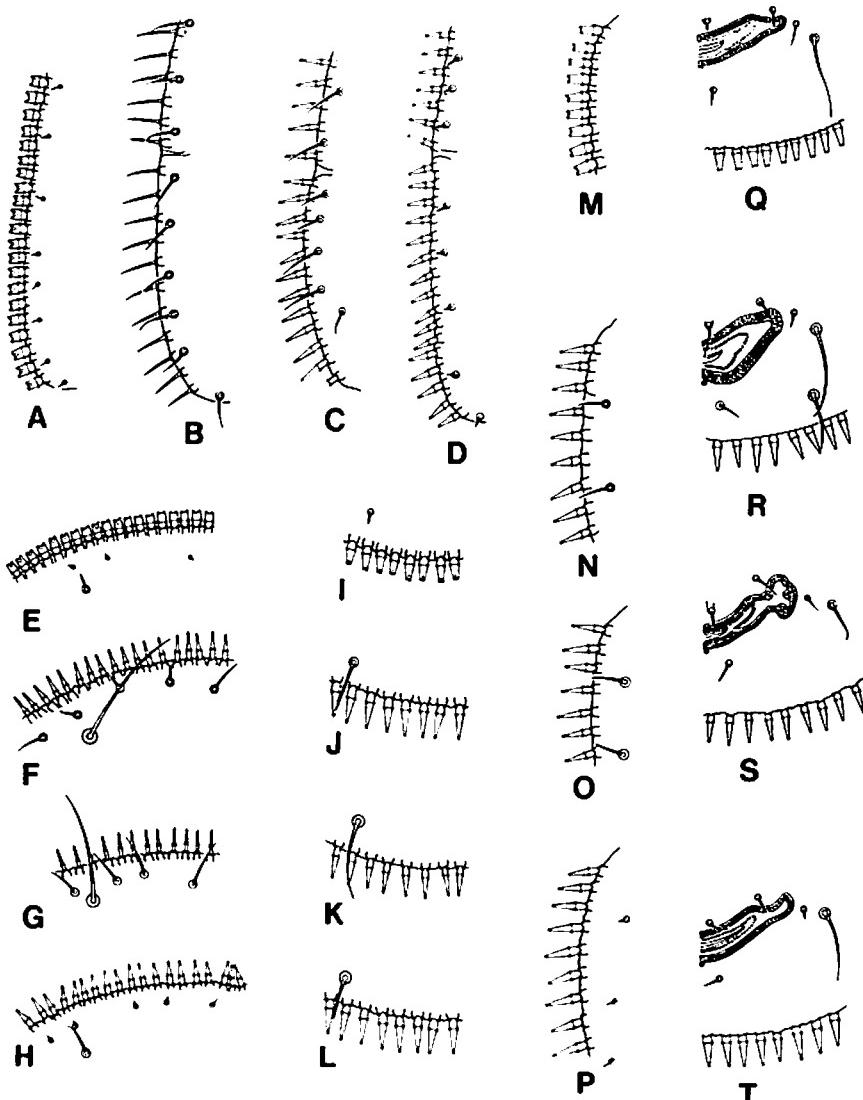


FIGURE 13. Second instar nymph of *Megatrioza palmicola* group. (A-D) Dorsal aspect of wingpads. (A) *M. palmicola*. (B) *M. kauaiensis*. (C) *M. molokaiensis*. (D) *M. mauliensis*. (E-H) Dorsal aspect of cephaloprothorax. (E) *M. palmicola*. (F) *M. kauaiensis*. (G) *M. molokaiensis*. (H) *M. mauliensis*. (I-P) Dorsal aspect of abdomen. (I, M) *M. palmicola*. (J, N) *M. kauaiensis*. (K, O) *M. molokaiensis*. (L, P) *M. mauliensis*. (Q-T) Ventral aspect of abdomen. (Q) *M. palmicola*. (R) *M. kauaiensis*. (S) *M. molokaiensis*. (T) *M. mauliensis*.

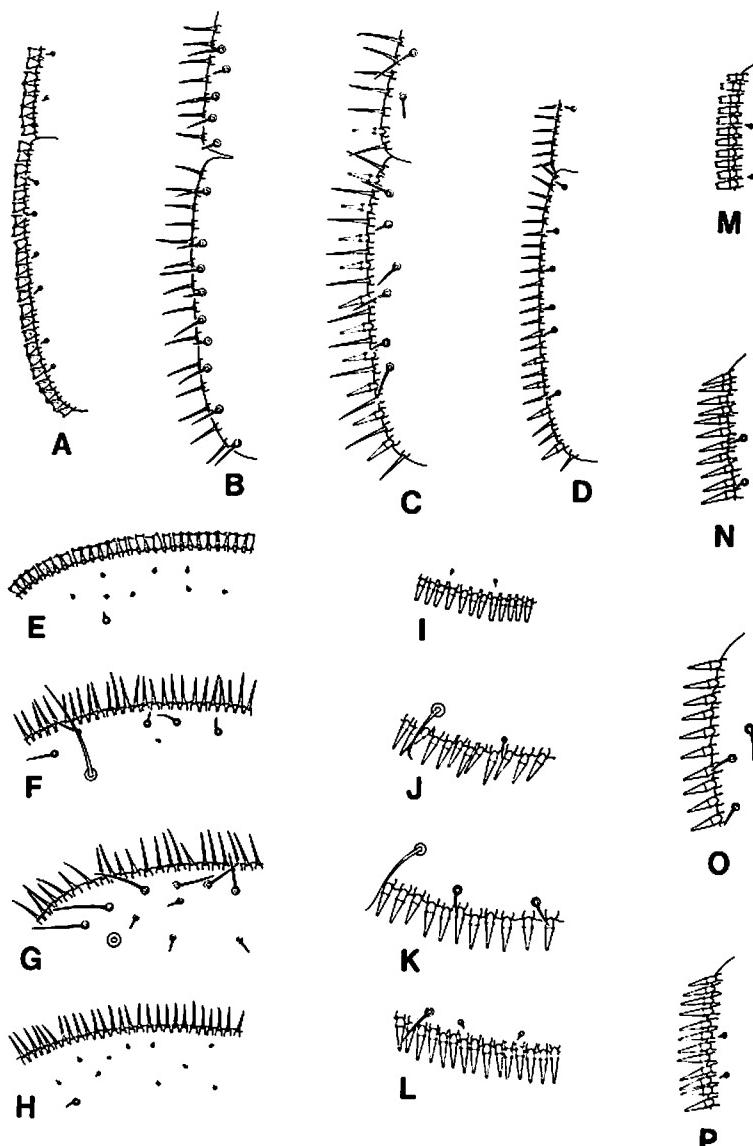


FIGURE 14. Third instar nymph of *Megatriozida palmicola* group. (A-D) Dorsal aspect of wingpads. (A) *M. palmicola*. (B) *M. kauaiensis*. (C) *M. molokaiensis*. (D) *M. mauiensis*. (E-H) Dorsal aspect of cephalothorax. (E) *M. palmicola*. (F) *M. kauaiensis*. (G) *M. molokaiensis*. (H) *M. mauiensis*. (I-P) Dorsal aspect of abdomen. (I, M) *M. palmicola*. (J, N) *M. kauaiensis*. (K, O) *M. molokaiensis*. (L, P) *M. mauiensis*.

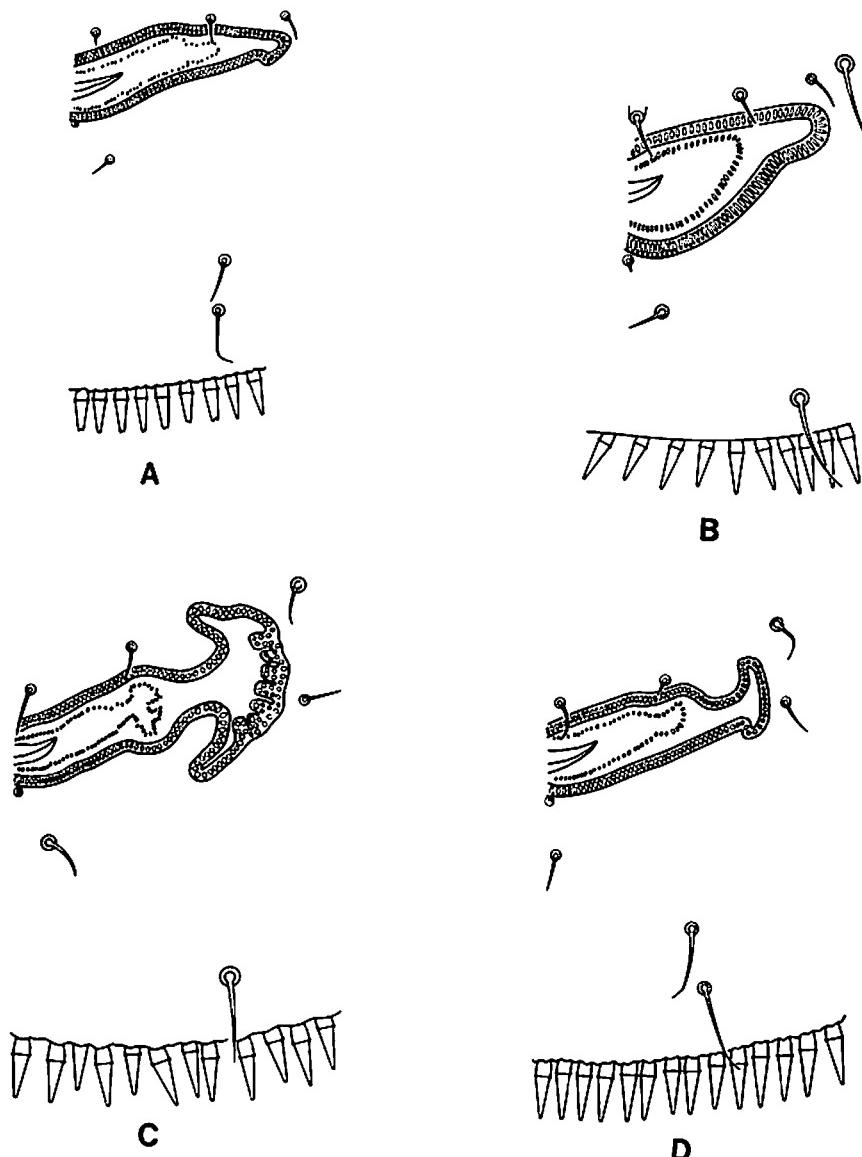


FIGURE 15. Third instar nymph of *Megatrioza palmicola* group. (A-D) Ventral aspect of abdomen. (A) *M. palmicola*. (B) *M. kauaiensis*. (C) *M. molokaiensis*. (D) *M. mauiensis*.

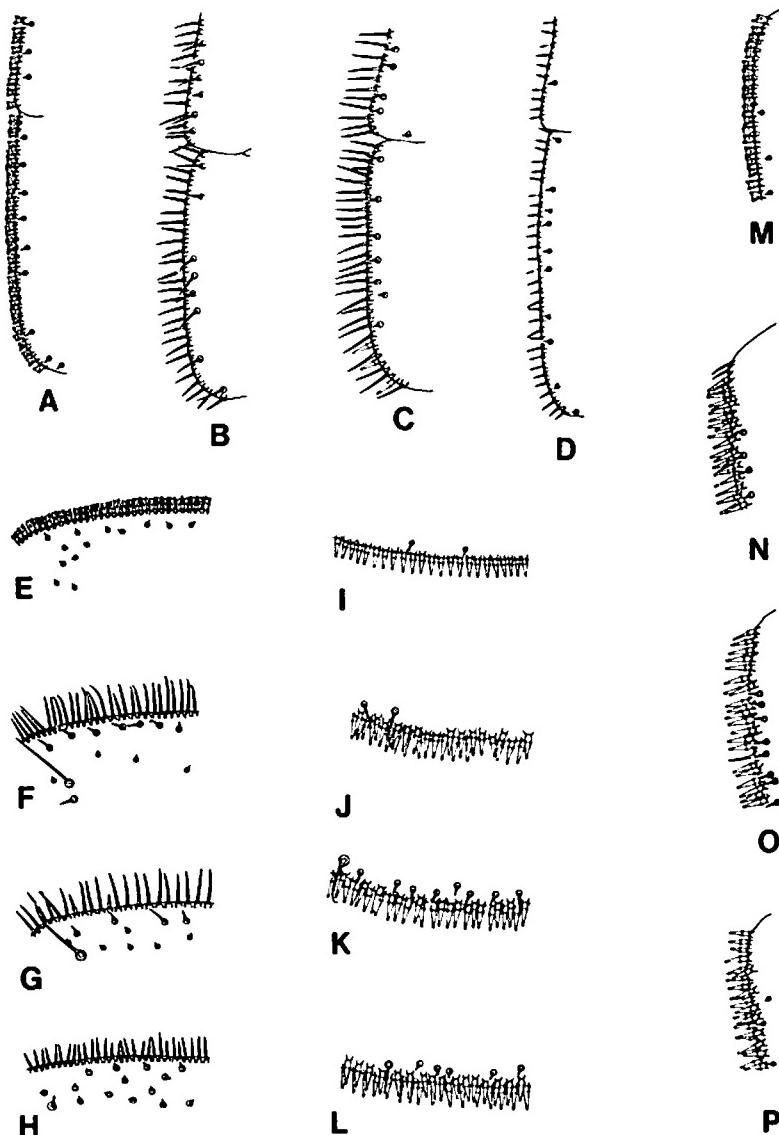


FIGURE 16. Fourth instar nymph of *Megatrioza palmicola* group. (A-D) Dorsal aspect of wingpad. (A) *M. palmicola*. (B) *M. kauaiensis*. (C) *M. molokaiensis*. (D) *M. mauliensis*. (E-H) Dorsal aspect of cephaloprothorax. (E) *M. palmicola*. (F) *M. kauaiensis*. (G) *M. molokaiensis*. (H) *M. mauliensis*. (I-P) Dorsal aspect of abdomen. (I, M) *M. palmicola*. (J, N) *M. kauaiensis*. (K, O) *M. molokaiensis*. (L, P) *M. mauliensis*.

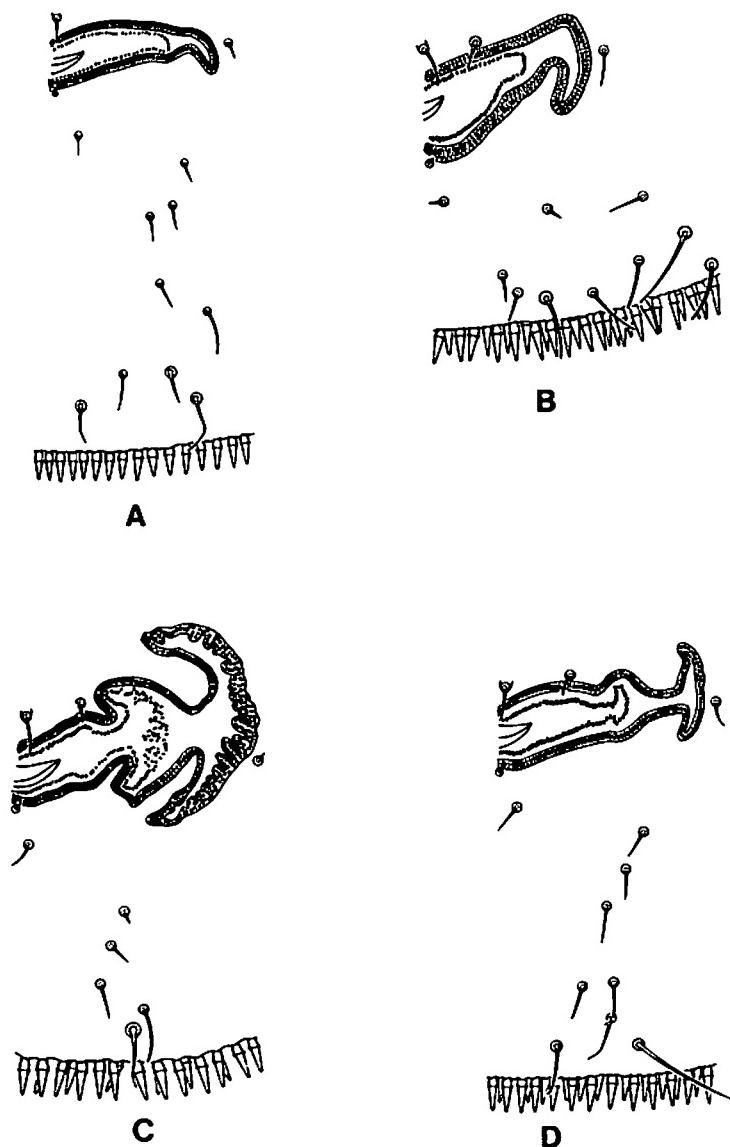


FIGURE 17. Fourth instar nymph of *Megatriozidae, palmicola* group. (A-D) Ventral aspect of abdomen. (A) *M. palmicola*. (B) *M. kauaiensis*. (C) *M. molokaiensis*. (D) *M. mauiensis*.

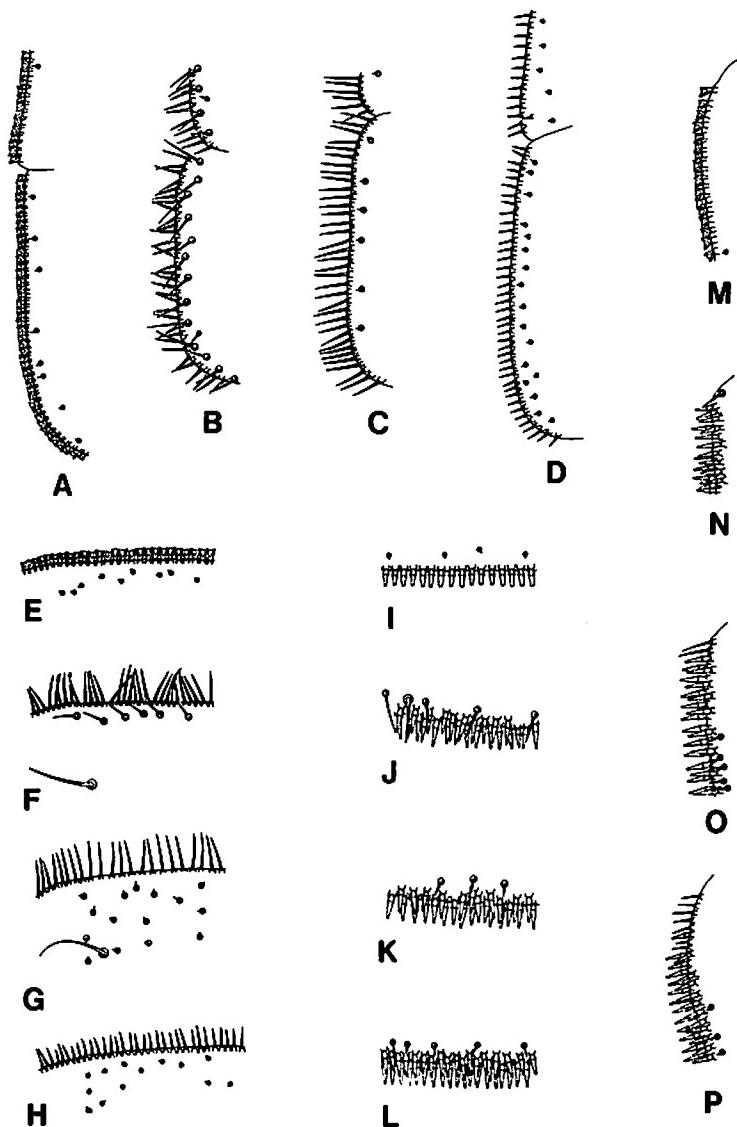


FIGURE 18. Fifth instar nymph of *Megatrioza palmicola* group. A-D) Dorsal aspect of wingpad. (A) *M. palmicola*. (B) *M. kauaiensis*. (C) *M. molokaiensis*. (D) *M. mauiensis*. (E-H) Dorsal aspect of cephalothorax. (E) *M. palmicola*. (F) *M. kauaiensis*. (G) *M. molokaiensis*. (H) *M. mauiensis*. (I-P) Dorsal aspect of abdomen. (I, M) *M. palmicola*. (J, N) *M. kauaiensis*. (K, O) *M. molokaiensis*. (L, P) *M. mauiensis*.

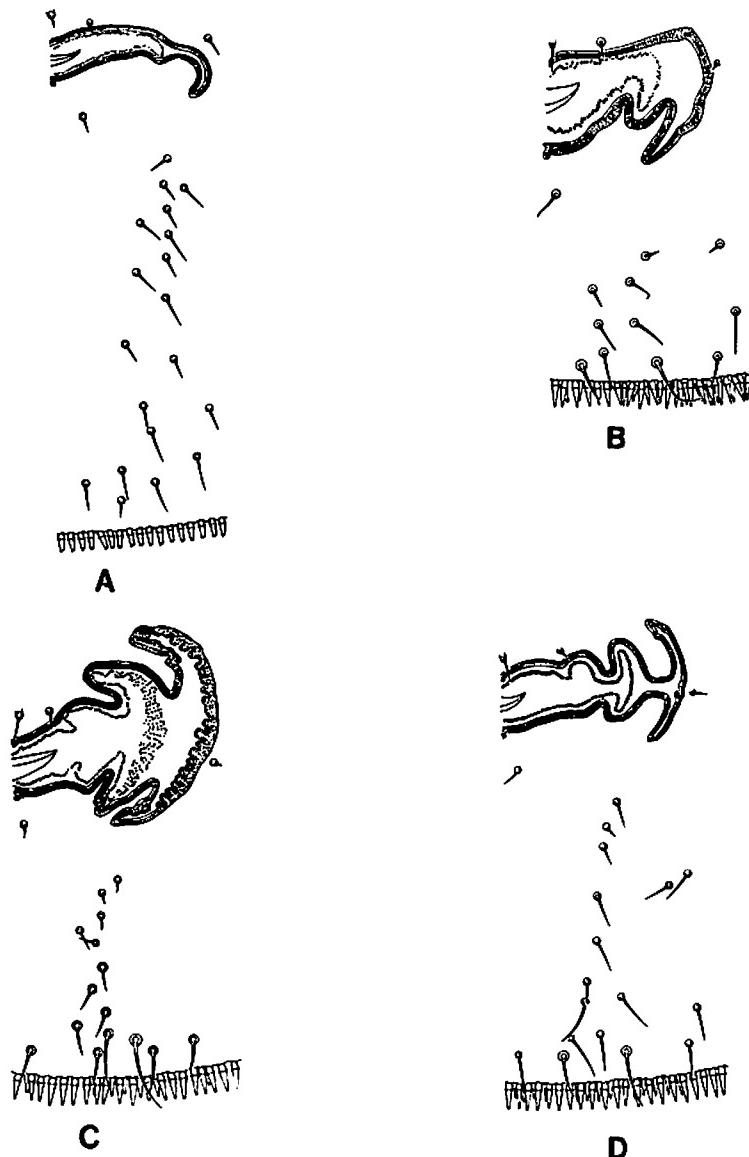


FIGURE 19. Fifth instar nymph of *Megatriozidae* group. (A-D) Ventral aspect of abdomen. (A) *M. palmicola*. (B) *M. kauaiensis*. (C) *M. molokaiensis*. (D) *M. mautiensis*.

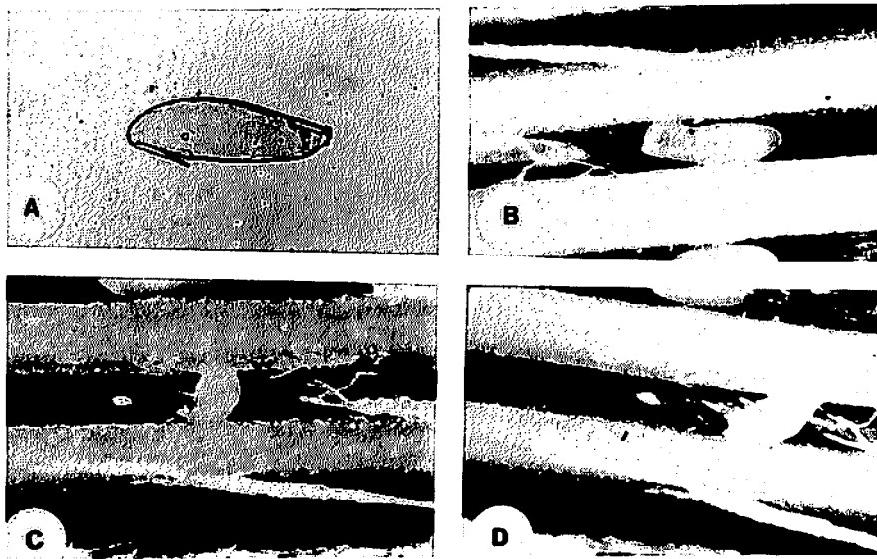


FIGURE 20. *Megatrioz kauaiensis*. (A) Egg. (B) Nymph inside chorion arched dorsally causing bulge near a line of weakness. (C) Nymph body partially eclosed, inclosed within epembryonic membrane. (D) Nymph body 3/4 exposed, legs free of epembryonic membrane.